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SYSTEMATICS OF THE NEOTROPICAL GENUS
CENTRADENIA (MELASTOMATACEAE)

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CENTRADENIA IS A WELL-DEFINED GENUS of subshrubs and suffrutescent perennial herbs comprising six taxa which are largely restricted to Mexico and Central America. The genus is unique among Mesoamerican Melastomataceae in having basally oblique leaves; pyriform, clavate, or dolabri-form seeds with a conspicuous lateral raphe; and pronounced anisophylly. Despite its small size, comparatively limited range, and remarkable diversity in androecial morphology, *Centradenia* has never been the subject of a comprehensive study. Because previous knowledge of the genus has been limited to regional floristic surveys, the limits and ranks of certain taxa have remained controversial. This study was undertaken in an effort to clarify the confusion by providing new information on chromosome numbers, ecogeographic distribution patterns, and the breeding systems of selected taxa. Based on the cumulative information obtained from these approaches together with an evaluation of morphological criteria, I here recognize four species (two of which are divided into two subspecies).

TRIBAL AND GENERIC CONSIDERATIONS

The genus *Centradenia* has been assigned by various authors to two of the five neotropical tribes of Melastomataceae with capsular fruits, the Tibouchineae (Krasser, 1893) and the Microlicieae (Cogniaux, 1891; Hooker, 1867; Triana, 1871). Tribal disposition of genera in the family has rested heavily on characters such as capsule symmetry, position of staminal appendages, prolongation of the connective, and seed shape. Krasser apparently emphasized the ventral position of appendages when he relegated *Centradenia* to the Tibouchineae; Cogniaux, Hooker, and Triana, however, gave greater weight to seed shape when they assigned it to the Microlicieae.

Tribal limits, especially among the Microlicieae, Rhexieae, and Tibouchineae, are not always clear. Consequently, tribal assignment often depends in large part upon which of the differences and similarities in stamens and seeds one chooses to emphasize. In a family such as the Melastomata-

ceae, where floral evolution has been extensive, one may logically conclude that the diverse floral types represent adaptations to different pollination systems. Therefore, caution must be used in any infrafamilial classification emphasizing floral features that appear to be evolutionarily labile. A focus on seemingly conservative characters such as the shape and surface patterning of seeds may provide a better approximation of affinities. This view is supported by the recent SEM study by Whiffin and Tomb (1972) of seed morphology in neotropical capsular-fruited Melastomataceae. Although their study essentially confirms the existence of five capsular-fruited tribes in the New World (see TABLE 1), it brings into question the delimitation of certain groupings as well as the disposition of selected genera. For example, the variously sculptured clavate or pyriform seeds of *Centradenia* have a conspicuous lateral raphe which is reminiscent of a modified bertolonioid seed but clearly unlike anything considered typical of the Microlicieae or Tibouchineae. Although current placement of *Centradenia* in the Microlicieae is, therefore, questionable, on the basis of present evidence I reject the expedients of tribal transfer or establishment of a new tribe to accommodate it.

A search for the closest generic relatives of *Centradenia* has contributed little to a clarification of its systematic position. *Centradenia* does not appear to be closely allied to any of the predominantly South American genera with which it was associated in the most recent familial monograph by Cogniaux (1891), or to have any close relatives among other Melastomataceae in Mexico and Central America. In describing *Centradeniastrum*, a poorly known ditypic genus of Colombia and Peru, Cogniaux (1908) placed it close to *Centradenia* in the Microlicieae, but he neglected to comment on the characters used to ascertain this relationship. Macbride (1941) also emphasized a close alliance between these two genera, but his suggestion to combine them seems unwarranted in view of their striking differences in vegetative, floral, and fruit characters. As with *Centradenia*, seed morphology of *Centradeniastrum* differs markedly from that of typical Microlicieae. The seeds of *Centradeniastrum album* Gleason are basically clavate with an asperulate testa; the broad expansion of the raphe into a flat wing on all sides of the embryo imparts a conspicuous pyramidal outline.

Although my study has not been sufficiently extensive to establish new tribal or generic limits, it seems evident that realignments will be needed as additional data become available. Based on present information, the seeds of *Centradenia* and *Centradeniastrum* are probably best interpreted as divergent modifications based on the bertolonioid theme. The relationships of these genera to each other or to members of the Bertoloniaceae is unclear and cannot be evaluated with confidence until other neotropical genera in the family are studied.

COMPARATIVE MORPHOLOGY

The following paragraphs provide a brief conspectus of the morphological features judged to be of taxonomic value in *Centradenia*. Herbarium

TABLE 1. Differences among the Neotropical Capsular-fruited Tribes of Melastomataceae.†

	CAPSULE SYMMETRY	STAMINAL APPENDAGE	CONNECTIVE PROLONGED BELOW THECAE	SEED SHAPE	SEED SURFACE PATTERN
MICROLICIEAE	terete or angulate	ventral	usually	oblong to cochleate	foveolate
TIBOUCHINEAE	terete or angulate	ventral	usually	cochleate	tuberculate
RHEXIEAE	terete	dorsal *	rarely **	cochleate	tuberculate, rugose, or costate
MERIANIEAE	terete or angulate	dorsal	rarely	cuneate or fusiform (often winged)	smooth, lightly foveolate, or minutely asperulate
BERTOLONIEAE	3-5-angled or -winged	ventral or dorsal	usually	cuneate, clavate, or pyramidate	tubercular-papillate to asperulate with a lateral raphe along the length of the seed

† Modified after Cogniaux (1891) and Whiffin & Tomb (1972).

* The stamens of *Pachyloma* have both dorsal and ventral appendages.

** *Pachyloma* invariably has prolonged connectives.

and fluid-preserved specimens have formed the basis for these descriptive notes, but most conclusions on variability are tempered by field observations and analysis of specimens prepared from cultivated material.

HABIT AND DURATION. All species of *Centradenia* have been described as suffrutescent herbs or well-developed shrubs; a few have even been reported as annuals on herbarium labels. Genetically, *C. paradoxa* and *C. grandifolia* are capable of attaining shrubby dimensions of 1 to 2 meters under optimal conditions in the field, but most individuals of the species that I have seen are best described as soft-woody subshrubs or suffrutescent perennial herbs with root systems that are fibrous and much-branched. Riedel (1957) notes that *C. grandifolia* and *C. floribunda* become as tall as 2 feet in cultivation, whereas *C. inaequilateralis* is generally smaller. All of these taxa are reportedly short-lived in cultivation, and *C. inaequilateralis* has been observed to behave as an annual under greenhouse conditions (Don, 1832; Wurdack, pers. comm.). This may suggest that these species are facultative annuals or biennials, with some individuals dying after one or two years of growth and others becoming established as perennials.

STEMS AND BRANCHING. The stems of *Centradenia grandifolia* are unique in being stout, conspicuously quadrangular, and typically winged at the junction of adjacent faces. In all other species the stems are slender and terete or subquadrangular, with one pair of narrow, flat to concave faces and a wider pair of rounded to convex faces. The branches of all species are alternate, more or less laxly disposed, and horizontally spreading from a central axis or strict to ascending with primary branches initiated in sympodial fashion from or near ground level.

LEAVES. Leaf arrangement in *Centradenia* is opposite and decussate, but the leaves on arching branches of *C. inaequilateralis* often assume a distichous orientation brought about by a twisting of the petioles. All species are characterized by a pronounced size dimorphism of paired leaves (anisophylly) such that the larger leaves alternate from one side of the stem to the other at each successive node. In *C. grandifolia*, *C. inaequilateralis*, and *C. paradoxa*, the smaller prevailing sessile leaf is frequently early deciduous, conveying a false impression of alternate phyllotaxy. Judging from its constancy in cultivated material, anisophylly in *Centradenia* undoubtedly has a genetic basis and is therefore of taxonomic value in characterizing the genus. Less is known about the functional significance of this peculiar foliar arrangement. Since *Centradenia* often inhabits sheltered or shaded habitats along forest streams or waterfalls, anisophylly may provide optimal accommodation of large and small leaves with minimal overlap, thereby enhancing light reception and increasing photosynthetic efficiency. If this speculation is correct, it would parallel the situation recently described for certain terrestrial anisophyllous species of *Columnea* (Gesneriaceae) by Morley (1973, 1974). Blades of the larger leaves are petiolate, plinerved, broadly to narrowly lanceolate, and generally asym-

metric at the base. Leaves with symmetric and asymmetric bases are not infrequently found on the same plant in such species as *Centradenia floribunda* and *C. inaequilateralis*. There are modal interspecific differences in leaf size, ranging from the smallest in *C. inaequilateralis* to the largest in *C. grandifolia*, but the susceptibility of this character to environmental modification makes it unreliable for a strict delineation of taxa.

PUBESCENCE. Three basic types of epidermal appendages may be recognized: smooth, unbranched, multicellular trichomes; glandular trichomes with multicellular stalks terminated by a globose cell; and appressed, translucent bacilliform structures that are actually clavate and multicellular when viewed under a light microscope. The latter, which measure about .25 mm. in length, are restricted to the young hypanthia and upper foliar surfaces of *C. inaequilateralis*. The presence, absence, and relative abundance of pubescence on stems, leaves, floral bracts, hypanthia, and petals vary considerably among individuals or populations. When a vestiture is present, multicellular trichomes predominate, but these are frequently associated with glandular hairs on peduncles of the inflorescence, floral bracts, hypanthia, and petal margins of most species. The length and posture of cauline trichomes are sufficiently variable to preclude taxonomic utility. In contrast, the length and attitude of hypanthial trichomes in *C. floribunda* and *C. inaequilateralis* are constant and diagnostic.

INFLORESCENCES. *Centradenia* is rather unique for a small genus in having both determinate and indeterminate inflorescences. Earlier workers (Gleason, 1958; Standley, 1938; Standley & Williams, 1963) described the inflorescence as solitary, few-flowered, or cymose. Although these descriptions are basically correct, a reappraisal of floral arrangements reveals greater diversity in both structural and developmental attributes than was previously thought.

The inflorescence of all taxa is derivable from the basic compound dichasial pattern characteristic of *C. grandifolia*. Borne in terminal and axillary positions, the dichasia vary greatly in size, compactness, and number of flowers. The branching pattern, like that of foliar arrangement, is opposite and decussate, with the primary axis producing a succession of nodes and subsidiary branches which terminate in simple dichasia. In decomposed structures with basal branches that are longer than those emanating from successive nodes, the inflorescence is commonly corymbiform in outline. The seemingly endless variations on the dichasial scheme are generated by amplification of the structural units already described, or by one or more of the following modifications:

- 1.) Reduction in length of primary and secondary axes.
- 2.) Terminal bud abortion of primary and/or secondary axes.
- 3.) Irregular abortion of floral buds.
- 4.) Complete suppression of secondary and/or tertiary branching.

The combined effects of the first three modifications listed above produce the inflorescence type typically encountered in *C. paradoxa*. It is gen-

erally diffuse and irregularly branched, and often consists of single flowers, paired flowers, and simple dichasia, collectively. At times, the degree of reduction is such that the inflorescence is superficially racemose, but differs in having basipetal rather than acropetal floral maturation.

The most significant modification of the compound dichasium is seen in *C. floribunda*, which exhibits a sparingly branched panicle consisting of two to six racemes diverging from common or proximal nodes at the base of the inflorescence. This structure is apparently derived by abortion of the primary axis and suppression of tertiary branching coupled with a shift from basipetal to acropetal floral maturation. Extreme reductions of an indeterminate structure such as the sparsely branched panicle often result in the short, solitary racemes so characteristic of *C. inaequilateralis*. Racemes may, in turn, be further modified by reduction of the central axis and abortion of floral buds to produce subfasciculate clusters and solitary flowers, respectively.

Despite their structure and developmental sequence, floriferous branches are always delimited by highly modified leaves (floral bracts) which subtend nodes and floral pedicels. These are thinly membranaceous or scale-like and rather inconspicuous. They differ sufficiently in form and vestiture to be of value in specific distinctions, but in most species they are caducous and are preserved only infrequently in herbarium material.

HYPANTHIUM AND CALYX. Mature hypanthia exhibit a series of subtle but diagnostic variations. They are terete or angulate, and range in shape from subcylindric through campanulate to urceolate or globose. Vasculature consists of eight \pm evenly spaced longitudinal ribs crowned by a circular ring conventionally called the torus. The four calyx lobes extending from the torus are broadly deltoid to truncate and are usually erect at anthesis and on fruiting hypanthia. The unusual hypanthia of *C. grandifolia* subsp. *grandifolia*, accrescent and somewhat bladderly, loosely envelop the ovary at maturity.

PETALS. Each of the four petals is inserted at a point on the torus opposing a stamen and alternating with a calyx lobe. The petals are dextrorsely convolute in bud and oriented in a horizontal plane or campanulate conformation when fully expanded. Although most petal characters are insignificant for specific delimitation, variations in size and color are useful in characterizing certain taxa. Petals of all species are broadly to narrowly obovate, entire to obscurely crenulate, and glabrous except for the margins which are sometimes fringed with smooth or glandular trichomes.

ANDROECIUM. The androecium of all species consists of eight poricidal stamens. In each species the stamens are differentiated into one of three size classes, ranging from strongly dimorphic through weakly dimorphic to subequal. Filament insertion on the torus is identical to that typically found in other genera of the family. The four stamens of the larger whorl

oppose the sepals and alternate with the four stamens of the smaller whorl which oppose the petals. In bud, filaments of all stamens are bent inward and downward, so that the ventral sides of the thecae face the interior surface of the hypanthial wall. The anthers of both whorls are smooth to undulate, 2-celled, and ventrally channeled. The connective is variously prolonged below the thecae and modified ventrally at the point of filament insertion into upturned or deflexed appendages of varying morphology. Connective length, and the size, shape, and color of anthers and appendages, provide valuable taxonomic criteria and undoubtedly have significance in the chain of events leading to pollination.

In expanded flowers the posture and spatial relationship of the style and stamens conform to one of two basic patterns. In *C. floribunda* subsp. *floribunda* and *C. paradoxa*, which have weakly dimorphic and subequal stamens, respectively, the anthers are connivent or slightly spreading around the more or less straight style, so that the stigma is situated among the anthers. In *C. paradoxa* the style often extends somewhat beyond the poricidal anthers.

In the second pattern the stamens are conspicuously dimorphic, and the style is permanently declined to one side of the flower. Filaments of the smaller staminal whorl are erect but somewhat twisted, so that the ventral surfaces of the thecae face away from the central axis of the flower. Filaments of the larger whorl may be erect or declined to that side of the flower occupied by the style. In either case, the geniculate bend in the stamens at the junction of filament and connective brings the anthers into a subparallel orientation more or less removed from the stigma. This complex androecial conformation recalls the pattern typically found in *Heterocentron*, a species of which is accurately illustrated by Ziegler (1925, fig. 70).

In general, declinate styles and strongly dimorphic stamens are correlated with prolonged connectives and elaborate appendages, whereas straight styles and connivent stamens correlate with reduction in length and complexity of these structures. The floral differences exhibited by these two groupings are basically the ones used by Cogniaux (1891) when he chose to divide the genus into two sections. Continued recognition of Cogniaux's infrageneric classification is untenable since it would demand the segregation into separate sections of the subspecies of *C. floribunda* recognized here. Furthermore, it would necessitate inclusion of *C. floribunda* subsp. *floribunda* and *C. paradoxa* in the same section. The similar floral features of these two taxa apparently represent convergent modifications which presumably enhance the probability of self-pollination. In this respect it is important to emphasize that they are more similar to outcrossing species with dimorphic stamens and declinate styles than they are to each other.

GYNOECIUM AND FRUIT. The essentially glabrous, 4-locular ovary is superior but fully enveloped by the hypanthium throughout its development. The apical portion of the ovarial wall may be glandular-ciliate as

in *C. paradoxa*, or variously elaborated distally into setose or ciliate outgrowths surrounding the stylar scar. The linear, glabrous style terminates in a punctiform stigma and assumes a stabilized posture ranging from more or less straight to declinate.

The fertilized gynoecium develops into a dry, thin-walled loculicidal capsule with axile placentation and usually persists on the infructescence long after all seeds have been dispelled.

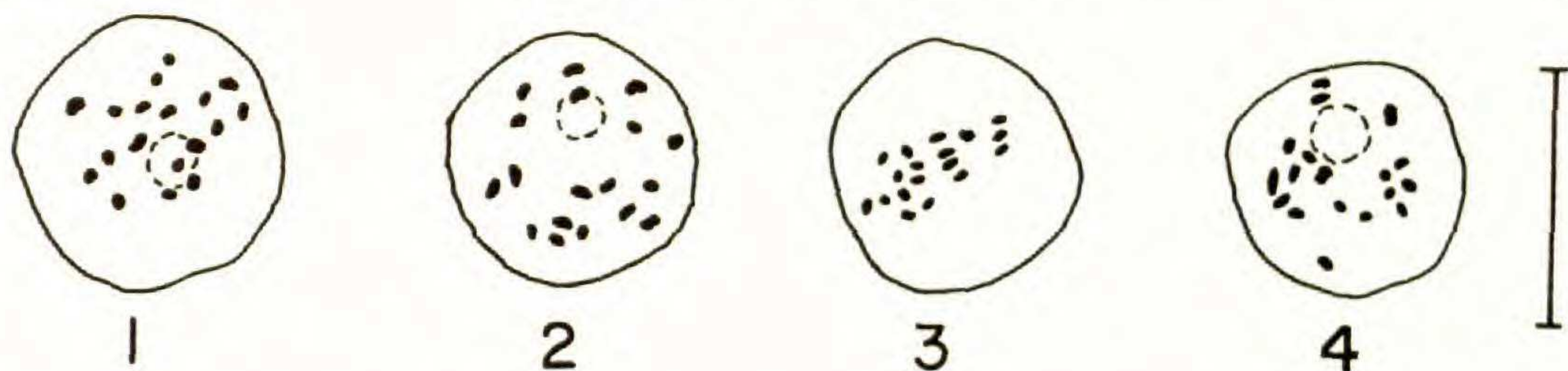
SEEDS. The seeds, which show little variation in size (0.5–1.0 mm. long), range in shape from narrowly pyriform to clavate or dolabriform, and consistently exhibit a longitudinal raphe extending along the length of the seed. Surface patterning ranges from papillate through muriculate or verrucose to echinate. The conservatism of seed characters in the family makes the diversity in *Centradenia* particularly valuable for drawing specific distinctions.

CYTOLOGY

Chromosome number determinations were made from diakinesis or metaphase I configurations in microsporocytes. Flower buds were fixed in the field for at least 24 hours in acetic ethanol (1:3), washed, and subsequently stored in 70 percent ethanol under refrigeration. The contents of immature anthers were squashed in acetocarmine. Voucher specimens for chromosome number determinations listed in TABLE 2 are deposited

TABLE 2. Chromosome Numbers in *Centradenia*.

TAXON	HAPLOID NUMBER	COLLECTION DATA
<i>C. floribunda</i> subsp. <i>floribunda</i>	$n = 18$	Cultivated: Longwood Garden (accession no. 631027), <i>Wurdack 2546</i>
<i>C. grandifolia</i> subsp. <i>grandifolia</i>	$n = 18$	Costa Rica. San José: 27 km. SE of Cartago, <i>Almeda 2677</i>
	$n = 18$	Costa Rica. San José: 9 km. N of San Isidro, <i>Almeda 2701</i>
	$n = 18$	Costa Rica. San José: 20–28 km. N of San Isidro, <i>Almeda 2704</i>
<i>C. inaequilateralis</i>	$n = 18$	Costa Rica. San José: 3–6 km. N of Las Nubes, <i>Almeda 2629</i>
	$n = 18$	Costa Rica. Alajuela/Heredia border: Varablanca, <i>Almeda 2652</i>
<i>C. paradoxa</i>	$n = 18$	Costa Rica. San José: 16–24 km. S of San Isidro, <i>Almeda 2692, 2693</i>



FIGURES 1-4. Camera lucida drawings of meiotic chromosome configurations in *Centradenia*. Scale line equals 12 micrometers (μm). 1 & 2, *Centradenia paradoxa*, $n = 18$, diakinesis; 3, *Centradenia inaequilateralis*, $n = 18$, metaphase I; 4, *Centradenia grandifolia* subsp. *grandifolia*, $n = 18$, diakinesis.

in the herbarium of the University of California, Los Angeles (LA) and/or the United States National Herbarium (US).

The haploid chromosome number for all taxa examined is 18 with normal meiosis (FIGURES 1-4). These counts are the first reports for *Centradenia grandifolia*, *C. inaequilateralis*, and *C. paradoxa*. The only previous chromosome count in *Centradenia* was published by Heitz (1926), who reported $2n = \text{ca. } 24$ for *C. floribunda*. Since that count was made from sectioned material, it may be erroneous and should be disregarded until reconfirmed. Unfortunately, Heitz cited no voucher specimens, so the identity of the plant he examined cannot be verified. The unpublished count of $n = 18$ for *C. floribunda* subsp. *floribunda*, which is reported here through the courtesy of J. J. Wurdack and M. L. Solt, casts further doubt on the number provided by Heitz and suggests that *Centradenia* may be homogeneous cytologically. Meaningful comparisons with other genera in the Microlicieae or Bertolonieae are not yet possible because of the paucity of published chromosome numbers for neotropical Melastomataceae. The only reliable published counts for members of these tribes are those of Davidse (1970), who reported a count of $n = 20$ for *Rhynchanthera paludicola* (J. D. Smith) Gleason and Sugiura (1940), who reported $n = 14$ for *Bertolonia maculata* DC. A haploid number of 18, however, is a relatively high basic number among angiosperms (Grant, 1971; Stebbins, 1971) and may indicate a polyploid origin for *Centradenia*.

BREEDING SYSTEMS

Information on the breeding system in *Centradenia* is limited to that derived from preliminary experimental manipulations of *C. grandifolia* subsp. *grandifolia* and *C. paradoxa* conducted under field conditions in Costa Rica. Following the procedures outlined elsewhere (Almeda, 1975), self-pollinations and complete staminal emasculations were performed on flowers of several individuals. In addition, a number of flowers were tagged and left open to potential pollinators in order to provide a comparative estimate of fruit set between open and artificially pollinated flowers. The primary objective of these enclosure experiments was to test for self-compatibility and apomixis. All emasculated, unpollinated flowers

TABLE 3. Summary of Artificial and Controlled Pollinations of Selected *Centradenia* Species.

SPECIES	NUMBER OF INDIVIDUALS TESTED	NO. OF FLOWERS TESTED			NO. OF FLOWERS SETTING FRUIT		
		OPEN POLLINA- TION	SELF POLLINA- TION	STAMINAL EMASCULA- TION	OPEN POLLINA- TION	SELF POLLINA- TION	STAMINAL EMASCULA- TION
<i>C. grandifolia</i>	14	42	40	32	40	2	0
<i>C. paradoxa</i>	10	30	43	20	29	39	0

of both species aborted approximately one week after peak stigmatic receptivity (see TABLE 3). This suggests that apomixis is not employed as a reproductive mechanism by these taxa. The results of artificial self-pollinations indicate that a strong incompatibility system is present in *C. grandifolia* but not in *C. paradoxa*, since the latter sets plump capsules with fully formed seeds comparable in all respects to controlled open-pollinated flowers. The structural and spatial attributes of floral parts in *C. grandifolia* and *C. paradoxa* are therefore significant since they act to promote outcrossing and inbreeding, respectively.

As noted under the discussion of morphology, the flowers of *Centradenia* species can be grouped into two categories according to the posture and spatial orientation of the style and stamens in relation to one another. Flowers of the outcrossing *C. grandifolia* have brightly colored petals ranging through various hues of pink. Upon floral expansion under mid-morning sunshine, the style becomes displaced to one side of the flower and assumes an abrupt apical curvature so that the stigma faces the central axis of the flower. The eight stamens comprising the androecium are dimorphic and are differentiated into two distinct whorls. The antepetalous stamens are comparatively small, yellow in color, and more or less erect at anthesis. The larger, magenta anthers of the antesepalous whorl are characterized by a geniculate bend at the point of filament insertion, which brings the anthers into a subparallel, platformlike conformation with apical pores extending well above or beyond the opposing stigma. The orientation of floral parts is such that the yellow appendages of the larger anthers are situated among the smaller, erect anthers. Hence, any disturbance of the small anthers elicits a concomitant movement of the larger anthers via the appendages. The spatial relationship of floral parts remains unchanged during the three to four day life of a flower. The poricidal nature of the anthers, together with their physical separation from the stigma, therefore suggests a system highly dependent on biotic manipulation for effective pollination. The flowers of *C. grandifolia* produce no detectable odor or nectar, but a visual signal consisting of the smaller yellow anthers and associated appendages apparently plays a key role in attracting pollen-seeking bees to the flower. I have observed bees of the genera *Bombus*, *Melipona*, and *Trigona* visiting the flowers of *C. grandifolia*. *Bombus* and *Melipona* always approach a flower facing the erect yellow anthers and then proceed systematically to probe each of them for pollen. *Trigona* is erratic and especially destructive in its pollen-foraging activities and often perforates or severs the larger anthers during its routine search for pollen among the smaller anthers. Because of their visitation method and small size, *Melipona* and *Trigona* rarely make physical contact with the stigma and are probably inconsequential as pollinators. In contrast, flower visitation by *Bombus*, the most frequent insect visitor noted in the course of my observations, is similar to the effective buzz pollination mechanism previously described for other Melastomataceae (Almeda, 1975; van der Pijl, 1939). Upon alighting on the landing platform of the flower provided by the larger subparallel stamens,

Bombus makes ample contact with the stigma, stamens, and appendages. Pollen discharge from the poricidal anthers is effected by a vigorous vibratory movement of the bee's thorax, accompanied by little or no perceptible wing movement. Therefore, the dimorphic androecium of *C. grandifolia*, like that of other Melastomataceae (Harris, 1905; Proctor & Yeo, 1973), has two important functions: the smaller, erect anthers provide pollen as an attractant, while the larger, geniculate anthers function in pollination. Although varying degrees of pollen viability have been reported for one or both sets of anthers in *Melastoma malabathricum* L. (Percival, 1965) and other angiosperm phylads with similar pollen presentation mechanisms (Bowers, 1975; Buchmann, 1974), I have found no significant reduction in pollen viability between the two types of anthers in any one flower of *C. grandifolia*.

Centradenia paradoxa exhibits the opposite extreme in floral morphology. The petals are invariably white and expand to a campanulate or bowl-like conformation. The yellow, subequal anthers have greatly reduced connectives and appendages and form a closely connivent cone around the straight style, which extends somewhat beyond the apex of the anthers. These features, in concert with the nodding posture of the flowers and the homogamous maturation of floral organs, appear to foster self-pollination. The jarring forces of wind and rain may also play a role in selfing, but the amount of autogamous reproduction in natural populations cannot be stated categorically at this time.

The natural pollinators of *Centradenia paradoxa* have not been seen during field studies. In *Dodecatheon* (Primulaceae), *Solanum* and *Lycopersicon* (Solanaceae) (all of which have flowers that are morphologically very similar to *C. paradoxa*), Macior (1964) has demonstrated that pollination is accomplished by bees which, while hanging in an inverted position, sift pollen from the pendent anther cone by rapid vibrations. Insect-mediated pollination of *C. paradoxa* is probably effected in a similar manner. The abundance and flight pattern of pollen vectors and the number of flowers per individual or inflorescence will, however, impose regulating influences on the relative amounts of geitonogamy (pollen transfer between flowers on the same plant) and xenogamy in natural populations.

Little is known about the reproductive biology of other species in the genus. If the structure and spatial relationship of floral parts can be used to make inferences, I would rank *Centradenia floribunda* subsp. *bernoullii* and *C. grandifolia* subsp. *brevisepala* as outcrossing species. The floral structure of *C. inaequilateralis* is reminiscent of an outcrosser, but the comparatively small flowers seem to close at dusk and during inclement weather, opening under the influence of bright light or sunshine. The effects of opening and closing movements on intrafloral pollen dispersion are unknown. Faegri and van der Pijl (1971) suggest that floral closing movements may serve as an effective pollination mechanism for self-compatible angiosperms. This speculation remains to be demonstrated for a species possessing poricidal anthers.

Centradenia floribunda subsp. *floribunda* is similar to *C. paradoxa* in having a straight style and more or less connivent anthers. The stigma is situated among the anther pores, but the flowers are held in erect fashion and apparently lack a mechanism to insure self-pollination in the absence of mechanical disturbance. According to Darwin (1876), *C. floribunda* sets abundant seed when artificially pollinated, but seed set is sporadic and unpredictable when plants are screened from potential pollinators.

GEOGRAPHY AND ECOLOGY

The distribution of *Centradenia* extends from Hidalgo, Mexico, south-eastward through Central America to Panama, with one species known from outlying stations in the Chocó lowlands on the Pacific coast of Colombia. This range parallels that of the monotypic genus *Schwackaea*, and to a lesser extent that of *Heterocentron*, which is centered in Mexico and northern Central America. These distribution patterns are noteworthy because almost all other neotropical genera in the family with species in Mexico and Central America have centers of diversity in South America.

The elevational amplitude for several taxa in *Centradenia* appears to be between 200 and 1900 meters, although *C. paradoxa* is presently unknown from elevations above 1200 meters, and *C. grandifolia* occurs primarily at elevations between 1300 and 2500 meters. All species are restricted in habitat, occurring most commonly on sheltered roadbanks, margins of streams and disturbed forests, or moist cliffs in the spray of waterfalls. *Centradenia floribunda* and *C. inaequilateralis* frequently maintain a foothold in the shallow soil accumulation of fissured boulders in or along streams. Field experience with three of the species leads me to suspect that partial shade and high moisture are requirements for their optimal development. Since wet, sheltered habitats are in themselves discontinuous elements of the landscape even in the tropics, the disjunct and sharply delimited population structure of each species is understandable. Large, inexplicable distributional gaps remain, however, for the comparatively wide-ranging species such as *C. grandifolia* and *C. inaequilateralis*. The typical subspecies of *C. grandifolia*, for example, occurs in eastern Mexico, western Guatemala, Honduras, and Costa Rica, but apparently is absent from what appear to be suitable habitats in Honduras, El Salvador, and Nicaragua.

Although the ranges of two or more species overlap in southeastern Mexico, western Guatemala, Honduras, and Costa Rica, I have been unable to find two species growing together or in closely adjacent populations. Sympatry would not be unusual in view of the similar habitat requirements and the overlapping elevational tolerances of several taxa.

The taxa exhibiting straight styles and connivent anthers have significant distributions in that they geographically replace their closest relatives which have flowers adapted for outcrossing. Thus, the outcrossing *C. floribunda* subsp. *bernoullii* of Honduras and El Salvador is replaced

by the typical subspecies in Guatemala and contiguous Mexico. Similarly, the outcrossing *C. grandifolia* subsp. *grandifolia*, which reaches its southern limit in the highlands of Costa Rica, is replaced both elevationally and geographically by *C. paradoxa* as one moves south and east of the Cordillera de Talamanca.

TAXONOMIC TREATMENT

Centradenia G. Don, Gen. Hist. Dichl. Pl. 2: 765. 1832.

Erect shrub, subshrub, or suffrutescent perennial, with strict and somewhat congested to loosely fastigate branching from a shallow fibrous root system. Distal cauline internodes glabrous to pubescent, terete, subquadrangular, or markedly quadrangular with carinate or prominently winged stem angles. Leaves opposite, decussate, petiolate, or sessile, strongly dimorphic to subequal in each pair, basically oblique or \pm symmetric, lanceolate, glabrate to copiously pubescent, plinerved. Inflorescence terminating main stems and upper lateral branches, basically a multiflowered (sometimes corymbiform) dichasium, but frequently becoming paniculate, racemose, or subfasciculate by reduction; bracts subtending floral pedicels and nodes of the inflorescence sessile, caducous, often thinly membranaceous and translucent. Flowers perigynous; hypanthium free from the ovary but fully enveloping it, urceolate to campanulate, terete or \pm quadrangular, 8-nerved, crowned by a circular vascular ring (torus) bearing sepals, petals, and stamens. Sepals persistent, erect to slightly spreading, broadly deltoid to triangular-ovate or truncate. Petals 4, free and spreading or connivent and somewhat cupulate, white or pink to magenta, fugacious, obovate, entire to remotely crenulate. Stamens 8; strongly dimorphic to subequal, composed of 4 larger stamens in an antesealous whorl and 4 smaller ones in an antepetalous whorl; filaments glabrous, compressed, and ligulate; anthers 2-celled, glabrous, linear-oblong, subulate or elliptic-ovate to obovate, and terminated by a solitary circular pore, connective prolonged below the thecae and variously modified ventrally into sessile or prolonged, upturned, vascularized appendages. Pollen white, prolate-spheroidal, 11.2–17.5 μm . in diameter, the three colporate apertures alternating with three pseudocolpi, sculpturing smooth to obscurely rugulate. Ovary superior, ovoid to obovoid, mostly glabrous but typically pubescent at the summit, quadrilocular with axile placentation; ovules numerous, anatropous, and borne on placental intrusions. Style glabrous, linear, straight or somewhat sigmoid and declinate; stigma punctiform. Capsule dry, semiwoody, loculicidal. Seeds narrowly pyriform to clavate or dolabriform, echinate (often glandularly so), verrucose to muriculate or papillate.

✓TYPE SPECIES. *Centradenia inaequilateralis* (Schlechtd. & Cham.) G. Don.

KEY TO THE SPECIES AND SUBSPECIES OF CENTRADENIA

- A. Inflorescence a short raceme or subfasciculate cluster of (1-)2-4(-6) flowers, axis typically less than 1 cm. long; hypanthia \pm quadrangular, sparsely pubescent, the trichomes smooth, antrorsely to widely spreading, and typically 0.5-1.5(-2) mm. long. 1. *C. inaequilateralis*.
- A. Inflorescence a multiflowered (often corymbiform) dichasium or a paniculate cluster of 2-6 elongate racemes diverging from one another \pm basally, axis typically (4-)6-18 cm. long; hypanthium \pm terete, often obscurely ribbed by longitudinal vascular strands, glabrous, glandular-puberulent, or beset with a mixture of antrorsely spreading smooth and glandular pubescence, the trichomes typically less than 0.5 mm. long.
- B. Stamens weakly dimorphic to isomorphic, differing primarily in size, otherwise similar in coloration and posture, stamens of the larger (antesepalous) whorl straight and \pm connivent around the straight style.
- C. Smaller leaf at each node sessile, usually early deciduous; anther thecae subulate, 3-4 mm. long, conspicuously undulate ventrally; connective prolonged basally at point of filament insertion into a dilated, facially flattened, triangular spur or tubercle; seeds clavate, beset with numerous glandular setose processes. Costa Rica, Panama, and Colombia. 2. *C. paradoxa*.
- C. Smaller leaf at each node petiolate, usually persistent; anther thecae elliptic-obovate, 1-1.5 mm. long, smooth to weakly channeled ventrally; connective prolonged basally into a \pm compressed bilobate or trilobate appendage; seeds narrowly pyriform to clavate, obscurely papillate to muriculate. Mexico and Guatemala. 3a. *C. floribunda* subsp. *floribunda*.
- B. Stamens distinctly dimorphic, differing primarily in size, posture, and coloration, stamens of the larger (antesepalous) whorl geniculate, forming a subparallel, platformlike conformation opposing the declinate style.
- D. Distal cauline internodes conspicuously quadrangular, strongly carinate or winged; smaller leaf at each node falcate to subulate, sessile or subsessile, often early deciduous; connective of the larger (antesepalous) staminal whorl prolonged ventrally into a dilated, upturned, bluntly bifurcate, clavate appendage. Mexico, Guatemala, and Costa Rica.
- E. Hypanthia globose to urceolate, broadest at the middle, accrescent and bladderly at maturity with conspicuous reticulate venation between the longitudinal vascular ribs; sepals ovate, apically rounded; petals pink; seeds clavate, beset with numerous setose processes. 4a. *C. grandifolia* subsp. *grandifolia*.
- E. Hypanthia campanulate, broadest distally at the torus, closely enveloping the ovary at maturity and lacking conspicuous reticulate venation between vascular ribs; sepals depressed-ovate, apically rounded, truncate or mucronulate; petals white, seeds clavate to dolabriform, beset with low, domelike processes. 4b. *C. grandifolia* subsp. *brevisepala*.
- D. Distal cauline internodes \pm terete to inconspicuously quadrangular but not strongly carinate or winged; smaller leaf at each node lanceolate, petiolate, usually persistent; connective of the larger staminal whorl prolonged ventrally into a compressed, upturned, \pm obtriangular or

linear-oblong appendage bearing two terminal caudiform processes. El Salvador and Honduras. 3b. *C. floribunda* subsp. *bernoullii*.

1. *Centradenia inaequilateralis* (Schlechtd. & Cham.) G. Don, Gen. Hist. Dichl. Pl. 2: 765. 1832. FIGURE 5.

Rhexia inaequilateralis Schlechtd. & Cham. Linnaea 5: 567. 1830. ✓TYPE: Mexico. Veracruz: Cuesta Grande de Chiconquiaco, *Schiede & Deppe 565* (holotype: presumably at B and destroyed during World War II; isotype: US!).

Rhexia parvifolia Schlechtd. Linnaea 13: 428. 1839. *nomen illegit.*, Art. 63, I.C.B.N.

Centradenia rosea Lindley, Bot. Reg. 29: 20. 1843. ✓TYPES apparently described from cultivated material originally collected at some unknown locality in Mexico. No type specimen can be located. (Lectotype: *pl. 20* of the protologue.)

Centradenia divaricata Kl. in Otto & Dietr. Allg. Gartenz. 19: 354. 1851. ✓TYPE: Central America, without further locality, *Warscewicz s.n.* (holotype: B, destroyed during World War II, photograph: GH!).

Centradenia oerstediana Kl. in Otto & Dietr. Allg. Gartenz. 19: 354. 1851. ✓TYPE: Costa Rica, at Turrialba, *Oersted s.n.* (holotype: presumably at B and destroyed during World War II).

Centradenia inaequilateralis var. *major* Cogn. in DC. Monogr. Phan. 7: 117. 1891. ✓TYPE: Mexico, Rio de Tanetze, *Galeotti 2963A* (holotype: BR; isotypes: F!, NY!, US!).

Erect, flimsy, arcuately branched, suffrutescent perennial 6 cm.–1 m. tall. Distal cauline internodes indistinctly quadrangular, becoming terete and inconspicuously striate in age. Nodal and internodal trichomes typically appressed-strigose but sometimes antrorsely spreading, smooth, mostly less than 0.5 mm. long, white to pink on juvenile growth but often turning tawny-brown with age. Plants anisophyllous. Principal leaves entire, basally oblique, subsessile or tapering to a petiole 0.5–4(–7) mm. long and 0.5 mm. wide, dark green or deeply pigmented above and below, randomly beset above with a sparse to copious mixture of appressed to antrorsely spreading trichomes of two lengths, the larger ones mostly 1–1.5 mm. long and the smaller ones usually less than 0.5 mm.; trichomes of the lower foliar surface uniform in length, ± restricted to elevated primary nerves. Larger leaf at each node narrowly lanceolate to sub-falcate, 1–5(–7.5) cm. long and 2–15(–20) mm. wide, attenuate apically, 3-plinerved. Smaller leaf at each node usually early deciduous, linear-oblong, 2.5–8(–14) mm. long and 0.5–3 mm. wide, acute apically, 1-nerved. Inflorescence terminal, but usually on lateral shoots, erect or somewhat pendent, consisting of (1–)2–4(–6) flowers borne on a sub-fasciculate cluster or short raceme mostly 1 cm. or less in length. Floral bracts sessile, greatly reduced and unlike principal leaves, early deciduous, 0.5–3 mm. long and 0.25–1.0 mm. wide, linear-lanceolate to falcate or narrowly spatulate, glabrous, entire but fringed apically with 3–5 smooth trichomes. Pedicels 1–8(–12) mm. long, mostly erect but becoming strongly cernuous in fruit. Hypanthia (at anthesis) campanulate, sparsely

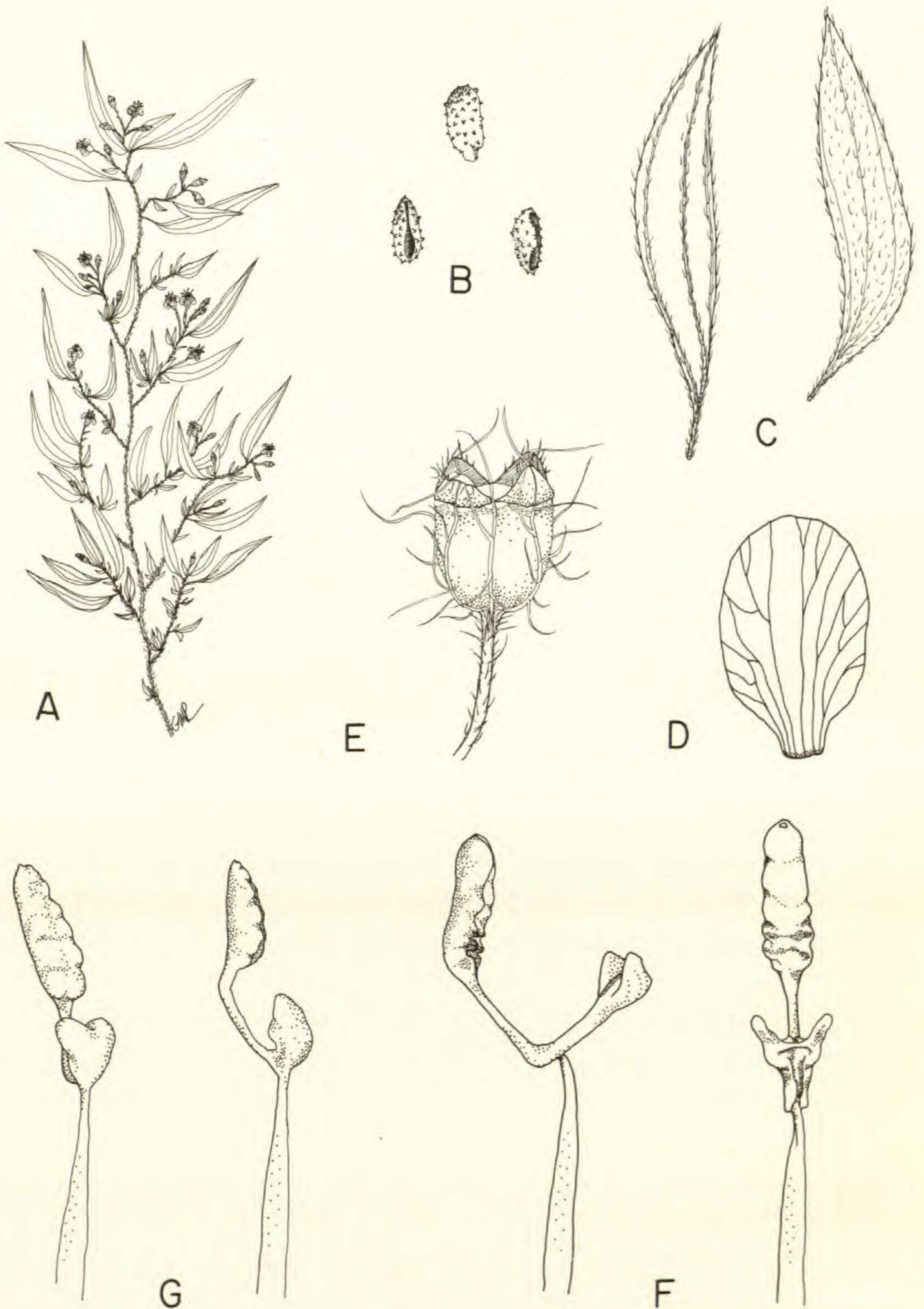


FIGURE 5. *Centradenia inaequilateralis*. A, habit, showing racemose and sub-fasciculate inflorescences, $\times \frac{1}{3}$; B, seeds, $\times 16$; C, representative leaves, abaxial surface showing three elevated nerves (left) and adaxial surface (right), $\times 1$; D, petal, $\times 5$; E, mature hypanthium, $\times 6$; F, larger stamens, lateral view showing prolonged connective and obtriangular appendage (left) and ventral view, $\times 10$; G, smaller stamens, lateral view (right) and ventral view (left), $\times 15$. (A-C, E from *Almeda 413*; D, F, & G from *Stone & Welden 3436*).

beset with antrorsely to widely spreading, flexuous trichomes 0.5–1.5(–2.0) mm. long, occasionally bearing additional crystalline bacilliform excrescences. Sepals (on mature hypanthia) erect, deltoid to ovate-triangular, glabrous within, sparsely pubescent without, ciliate, and tipped with a trichome equaling or exceeding the sepal proper, 1–1.5(–3) mm. long, 1.5–2(–3) mm. wide. Petals white, often fading to pale pink, glabrous, oval to narrowly obovate, sometimes fringed with glandular trichomes, 4–7(–9) mm. long, 2.5–5 mm. wide. Stamens dimorphic. Larger stamens: geniculate, filaments 2.5–4 mm. long; anthers pink, linear-oblong, 1–3 mm. long and 0.5 mm. wide, thecae undulate; connective 1–2.5 mm. long; appendages yellow, erect to ascending-obconic, barely emarginate to bilobed apically, 1.5–2.5 mm. long, 1 mm. wide distally. Smaller stamens: erect or ascending, filaments 2.5–3.5 mm. long; anthers pale yellow, linear-oblong to ovoid, 0.5–1 mm. long, 0.5 mm. wide, thecae gently undulate; connective 0.5–1 mm. long, appendage yellow, erect, ellipsoid to obconic, shallowly bilobed apically, 0.5 mm. long, 0.5 mm. wide. Pollen 11.2–12.5 μm . in diameter. Ovary ovoid, glabrous basally but apically setose. Style 3–4 mm. long, declinate, and opposing the geniculate whorl of stamens. Hypanthia (at maturity) campanulate, \pm quadrangular, often deep red in color, 2–3.5 mm. long, 2–3.5 mm. wide. Seeds narrowly pyriform to clavate, muriculate, mostly less than 0.5 mm. long. Chromosome number: $n = 18$.

Flowering: all year.

DISTRIBUTION. Widespread but localized at elevations of 200 to 1900 meters from southeastern Mexico to north-central Guatemala, east to western and central Honduras and south through central and western Nicaragua, to Costa Rica and Panama.

REPRESENTATIVE SPECIMENS. Costa Rica. ALAJUELA: C. R. #9 ca. 7.6 km. n. of Varablanca, *Almeda* 413 (DUKE); Piedades de San Ramón, *Brenes* 4763 (CR, F, MO, NY); calera de San Ramón, *Brenes* 5887 (CR, F, MO, NY); e. slopes of Poás along Hwy. #9, n. of Varablanca, *Luteyn* 3891 (DUKE); 2 km. w. of La Marina, Llanura de San Carlos, *Molina et al.* 17371 (F, GH, NY, US); n. slope of Cordillera Central, *Skutch* 3114 (A, MO, NY, US); San Luis de Zarcero, *Smith* 122 (US); near San Ramón, *Tonduz* 17844 (CR, GH, MICH, US); ca. 1–9 km. n. of Cinco Esquinas, *Wilbur, Almeda, & Luteyn* 15742 (DUKE); ca. 4 mi. n. of Varablanca on road to Sarapiquí, *Wilbur & Teeri* 13706 (DUKE, F, MICH, MO). ALAJUELA/HEREDIA BORDER: roadbanks along C. R. #9 ca. 7 km. beyond Varablanca, *Almeda* 2652 (LA, US). CARTAGO: road to Siquirres ca. 7.1 km. nw. of road junction at Turrialba, *Almeda* 557 (DUKE); trail from grounds of Interamerican Institute of Agricultural Sciences, Turrialba, *Carlson* 3353 (F, GH); river bank at Turrialba, *Godfrey* 66325 (FSU, MO); pasture overlooking Rio Tambor 3 km. e. of Cachí, *Lent* 858 (NY); s. of Las Vueltas, Tucurrique, *Tonduz* 13065 (US); bank just west of Santa Cruz ca. 10 mi. nw. of Turrialba, *Wilbur & Teeri* 13772 (DUKE, GH, MICH, MO, NY). GUANACASTE: vicinity of Monteverde, *Feinsinger s.n.* (CR); El Silencio Tilarán, *Jimenez* 393 (CR, F); Los Ayotes near Tilarán, *Standley & Valerio* 45397 (F, US); pasture adjoining main road and Chomogo trail near headwaters of Rio Guacimal above Monteverde, *Stone & Welden* 3436 (CR, DS, DUKE, MICH, MO); se. slopes of Volcán Mira-

valles near Rio Naranjo, *Wilbur & Almeda 16618* (DUKE); 5 km. e. of Tilarán above Laguna de Arenal, *Williams & Williams 25098* (LL); ca. 2–5 km. se. of Monteverde, *Burger & Gentry 8724* (CR). HEREDIA: ca. 7 km. beyond Varablanca on road to Puerto Viejo, *Almeda & Flowers 2406* (DUKE); waterfall along road between Varablanca and Cariblanco, *Davidse & Pohl 1277* (CR, MO); 7.1 km. n. of Varablanca on Hwy. #9, *Luteyn 599* (DUKE, F); above La Paz on road from Varablanca to Puerto Viejo, *Stone & Welden 3404* (DUKE); slopes above Rio Para Blanco on lower slopes of Cerro Zurquí ca. 7 km. ne. of San Josecito, *Wilbur & Luteyn 18636* (DUKE). LIMON: Rio Pacuar, Comarca de Limon, *Donnell Smith 6550* (US); open banks near Rio Toro Amarillo in vicinity of Guápiles, *Godfrey 66323a* (FSU, MO). PUNTARENAS: vicinity of Monteverde, *Almeda 664* (DUKE). SAN JOSÉ: C. R. #216 ca. 3–6 km. beyond Las Nubes near Cascajal, *Almeda 2629* (DUKE, F, LA, MO, NY, UC, US); Rio Claro along trail to Guápiles, *Burger 3869* (CR, F, NY, US); La Verbena near Alajuelita, *Tonduz 8913* (CR, F, US); ca. 4–4.5 km. n. of San Isidro de San Jose, *Utley & Utley 406* (DUKE); Alto La Palma ca. 7.5 mi. n. of San Vicente, *Wilbur & Almeda 16679* (DUKE); ca. 12 mi. nne. of San Vicente de Moravia, *Wilbur & Almeda 16880* (DUKE). Guatemala. ALTA VERAPAZ: near Finca Sepacuite, *Cook & Griggs 222* (US, photo at F); trail from Senahú to Actala, *Maxon & Hay 3336* (GH, NY, US); Pantín, below Tamahú, *Standley 70557* (F). BAJA VERAPAZ: brook bank at Finca Civija, *Sharp 4647* (F, MEXU). SAN MARCOS: canyon s. of San Marcos toward Castalia, *Williams et al. 26114* (F). Honduras. CORTÉS: Cuyamel, *Carleton 465* (US). COMAYAGUA: Montaña El Cedral, Cordillera Montecillos 20 km. s. of Siguatepeque, *Molina 8031* (F, NY); Quebrada Montanuelas, *Molina 10860A* (F, LL, NY, US). SANTA BARBARA: San Pedro Sula, *Thieme 5229* (F, GH, US). Mexico. VERACRUZ: near Orizaba, *Bilimek 211* (GH, NY, US); Valle de Córdoba, *Bourgeau 1964* (ENCB, GH, MICH, MO, NY, US); Córdoba, *Greenman 201* (F, GH, NY, US); Fortín de las Flores, *Kerber 314* (MICH, US); Zacuapan and vicinity, *Purpus 2304* (F, GH, MO, NY, UC, US); barranca de Tenampa, Zacuapan, *Purpus 5805* (UC); region of Santiago Tuxtla, *Sousa 2253* (MEXU); Santa Rosa, municipio de Teocelo, *Ventura 877* (DS, ENCB, LL); El Mirador, municipio de Totutla, *Ventura 5063* (ENCB); Vista Hermosa, municipio de Jilotepec, *Ventura 9625* (ENCB). Nicaragua. GRANADA: Volcan Mombacho, *Baker 2450* (A); summit of Mombacho, *Grant 797* (GH, NY); wet trail on Mombacho volcano, *Maxon, Harvey, & Valentine 7762* (US); rain forest on Mombacho, *Narvaez 3926* (GH, MICH, MO, NY, UC); crater rim on Volcan Mombacho, *Wilbur & Almeda 16582* (DUKE). JINOTEGA: San Rafael del Norte, *Miller & Griscom 73* (US). MANAGUA: vicinity of Managua, *Garnier 936* (US); Sierras de Managua, *Grant 1014* (GH, MICH, NY). MASAYA: region of Las Nubes, Sierra de Managua, *Standley & Garnier 8122* (F). MATA-GALPA: river course near Jinotega, *Grant 7297* (GH, NY); near El Porvenir, Cordillera Central, *Molina 20525* (DUKE, F, MO, NY); Cerro El Picacho, finca Santa Maria de Ostuma, Cordillera Central, *Williams et al. 29183* (F, GH, NY, US). Panama. BOCAS DEL TORO: 5 mi. s. of Junction of Rios Changuinala and Terebé, *Lewis et al. 864* (MO); Rio Terebé between Queb. Treglo and Puerto Palenque, *Kirkbride & Duke 523* (MO, NY). CHIRIQUÍ: w. side of Cerro Pando, *D'Arcy 6652* (MO); 5.2 mi. nw. of El Hato del Volcan, *Luteyn 830* (DUKE, F, MICH); vicinity of El Boquete, *Maxon 5057* (US); forests around Boquete, *Pittier 3040* (F, US). COCLÉ: hills n. of El Valle, *Allen 3907* (GH, MICH, MO, NY, US); hills ne. of El Valle de Antón, *Lewis et al. 1699* (GH, MO, US); El Valle, *Croat 22978* (MO); 2 mi. n. of El Valle, *McDaniel 8288* (DUKE, FSU); w. slopes

of Cerro Pajita in crater of El Valle de Antón, *Wilbur & Almeda 15609* (DUKE, MO).

This is the most widespread and frequently collected species. As noted by Standley and Williams (1963), although it is surprisingly uncommon through most of its range, it appears to be especially abundant in Costa Rica: over half of the approximately 300 specimens examined are from that country.

Centradenia inaequilateralis exhibits some intricate patterns of variation with respect to such features as stature, pubescence, foliar size, and the degree to which the asymmetry of foliar bases is expressed. Variation involving these characters often occurs in combinations that give individuals or populations a distinctive facies. Despite previous attempts to catalogue this variability, there is no justification for taxonomic fragmentation at any level since none of the variants can be correlated with any consistent geographical or ecological pattern. A few of the variants are sufficiently distinct or recur with ample frequency, however, to warrant brief mention. The variety *major* described from Mexico by Cogniaux, has unusually large, thin leaves, mostly 6.4–7.5 cm. long and 1.7–2 cm. wide, with a sparse and inconspicuous trichome covering. This form appears to be nothing more than an environmentally induced modification since comparable individuals growing under highly shaded conditions have been noted at disjunct localities in Costa Rica and Panama. At the other end of the spectrum, conspicuously dwarfed variants have been found in central Panama (*Lewis et al. 1699*). These variants, collected along the edge of disturbed forests, range in height from 4–15 cm. and have very short internodes, with leaves barely exceeding 2 cm. in length. Similar individuals have also been gathered in central Costa Rica (*Wilbur & Almeda 16880*), where they were found growing epipetrically along a stream bank. Whether these dwarfed variants represent a genetic race remains to be demonstrated, but the array of intermediates bridging them with the larger-leaved forms mentioned above suggests that much of the variation is habitat-mediated.

Another distinctive variant with copious, spreading pubescence on the leaves, stems, and hypanthia is known from Nicaragua (*Grant 7297*) and Costa Rica (*Wilbur & Almeda 16618*). This variation may well have a simple genetic basis comparable to that described elsewhere for *Monochaetum floribundum* (Schlechtd.) Naud. and is perhaps nothing more than a sporadically occurring biotype (Almeda, 1975).

Aside from its simple inflorescence, comparatively small leaves, and diagnostic staminal features, *C. inaequilateralis* can be distinguished from its congeners by the \pm quadrangular hypanthia beset with flexuous trichomes. One anomalous collection from Nicaragua (*Miller & Griscom 73*) has hypanthia with narrowly winged angles reminiscent of the mature hypanthia in several species of the South American genus *Pterogastra*. Although this character has been much used as a taxonomic character in

Pterogastra, it appears to be nothing more than a developmental aberration in *Centradenia*.

2. *Centradenia paradoxa* (Kränzlin) Almeda, comb. nov. FIGURE 6.

Tibouchina (?) *paradoxa* Kränzlin, Vierteljahr. Naturf. Gesell. Zürich 76: 147. 1931. TYPE: Costa Rica, Bords du Rio Naranjo, Versant Pacifique, 200 m., March 1893, *Tonduz 7628* (holotype: presumably at B and destroyed during World War II; isotypes: F!, GH!, US!).

Centradenia maxoniana Gleason, Bull. Torrey Bot. Club 65: 571. 1938. TYPE: Panama. Chiriquí: between Hato del Jobo and Cerro Vaca, 700–1000 m., *Pittier 5414* (holotype: US!, photograph: NY!).

Erect, laxly branched shrub or subshrub 0.5–2(–3) m. tall with slender, ± zigzag, flexuous stems. Cauline internodes terete to subquadrangular, copiously beset with appressed, smooth, subulate trichomes (1.0–1.5 mm. long), often intermixed with or replaced by antrorsely spreading, glandular trichomes (0.5–1.0 mm. long) on juvenile growth. Plants strongly anisophyllous. Principal leaves entire, basally asymmetric, dark green above, paler below. Larger leaf at each node linear-lanceolate to somewhat falcate, (4–)5–18 cm. long and 1–3.5(–4.5) cm. wide, acute to attenuate apically, 3–5-plinerved, the three central nerves prominent below, the marginal pair usually depressed and inconspicuous, randomly beset with appressed, smooth trichomes (0.5–1.0 mm. long) on and between impressed primaries on both surfaces, sessile or with petioles 1–4(–6) mm. long and 1–2(–3) mm. wide. Smaller leaf at each node mostly early deciduous, sessile, narrowly subulate to acicular or falcate, 7–13 (–15) mm. long and 0.5–1.0 mm. wide, sparsely pubescent to glabrate. Inflorescence terminal, commonly on lateral shoots, typically a pendent or nodding, multiflowered, variously reduced dichasium mostly 4–15 cm. long, peduncles ± quadrangular, glandular-pubescent. Floral bracts sessile, thinly membranaceous and translucent, markedly reduced in size upward, early deciduous, 1.5–7(–9) mm. long and 1–3 mm. wide, linear-lanceolate to subulate, often navicular and sheathing immature buds or their pedicels, entire, glandular-puberulent. Pedicels 1.5–5 mm. long, usually cernuous at anthesis bringing the flowers to an inverted position, beset with trichomes like the peduncles of the inflorescence. Hypanthia (at anthesis) cylindrical-campanulate, beset with simple and/or glandular, antrorsely spreading trichomes mostly less than 0.5 mm. long. Sepals (on mature hypanthia) erect, ± triangular, varying to depressed-ovate, glabrous within, sparsely puberulent to glabrous without, remotely ciliate, 1–1.5 mm. long and 1–2 mm. wide at base. Petals white, linear-oblong to narrowly obovate, entire, glabrous but minutely glandular-ciliate, 5–7 mm. long and 3–4 mm. wide. Stamens subequal, alternately differing in length, straight, ± connivent around the style; thecae yellow, linear-subulate, markedly convoluted and channeled ventrally along the connective which is modified basally (at point of filament insertion) into a dilated, facially flattened, triangular spur or tubercular appendage.

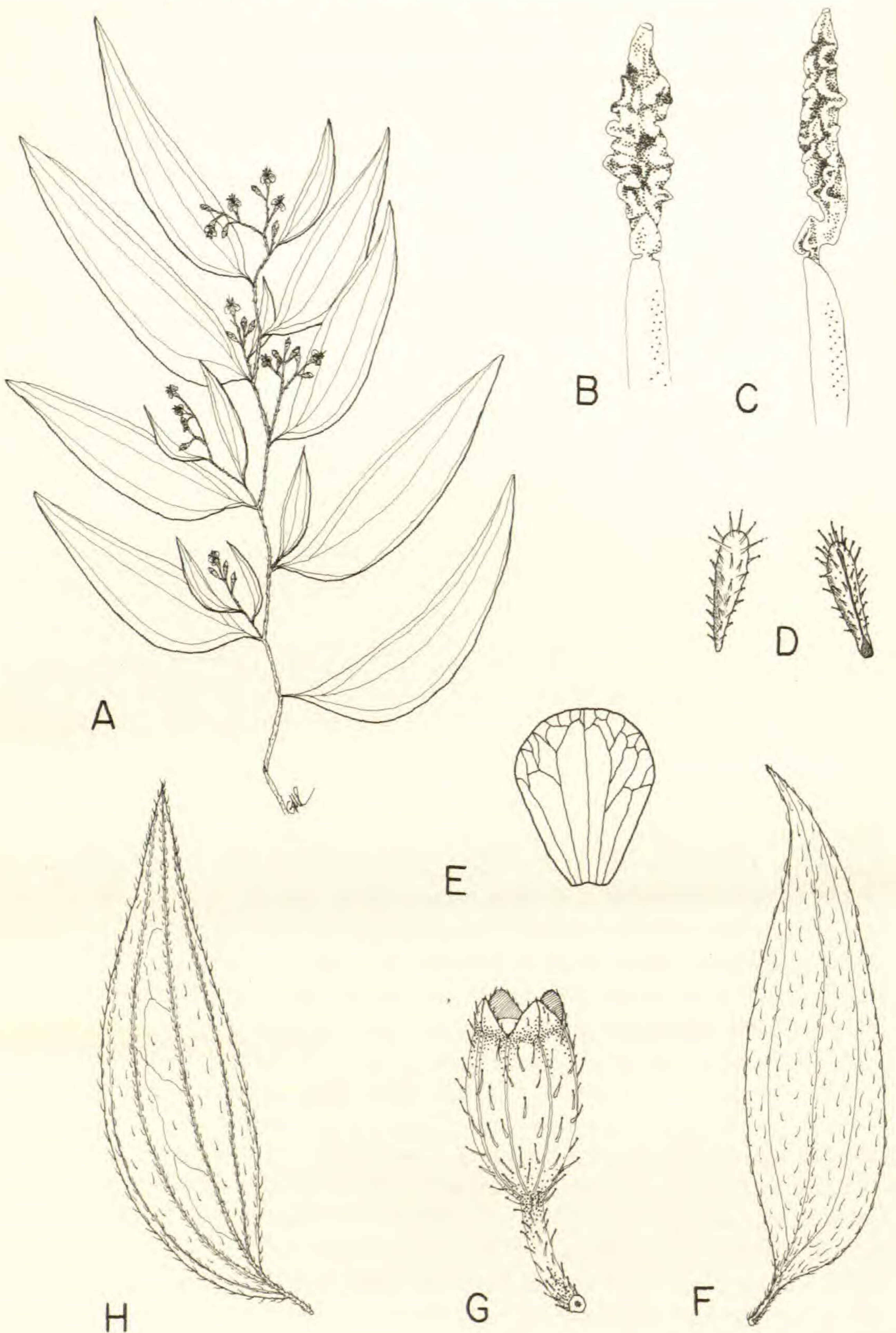


FIGURE 6. *Centradenia paradoxa*. A, habit, $\times \frac{1}{3}$; B, smaller stamen, ventral view, $\times 8$; C, larger stamen, lateral view, $\times 8$; D, seeds, dorsal view (left) and ventral view (right), $\times 30$; E, petal, \times ca. 3; F, leaf, adaxial surface, $\times \frac{1}{2}$; G, mature hypanthium, $\times 4$; H, leaf, abaxial surface, $\times \frac{1}{2}$. (A, F, H from Allen 112; B-E, G from Wilbur & Almeda 15607).

Larger stamens: filaments 2–3.5 mm. long; anthers 3–4 mm. long and 0.5 mm. wide; connective and appendage each 0.5–1.0 mm. long. Smaller (antepetalous) stamens: filaments 1–2.5 mm. long; anthers 2–3.5 mm. long and 0.5 mm. wide; connectives and appendages like those of larger stamens. Pollen 11.2–12.5 μ m. in diameter. Ovary ovoid to obovoid, glandular-ciliate at the summit but otherwise glabrous. Style slender, 6–8 mm. long, equaling or exceeding the larger stamens, straight and terminated by a subcapitate stigma. Hypanthia (at maturity) 4–7 mm. long, 3–6 mm. wide. Seeds clavate, usually less than 0.5 mm. long, covered with numerous glandular setose projections. Chromosome number: $n = 18$.

Flowering: December–March.

DISTRIBUTION. Puntarenas and San José provinces on the Pacific side of the Cordillera de Talamanca in southwestern Costa Rica, extending southeastward in disjunct fashion to Chiriquí and Coclé provinces in Panama and south to the Chocó lowlands of Colombia, from sea level to 1200 meters.

REPRESENTATIVE SPECIMENS. **Colombia.** CHOCÓ: Alto de Buey, *Gentry & Forero 7291* (MO); along stream at Bahia Solano, *Haught 5529* (NY, US). **Costa Rica.** PUNTARENAS: Cienega de Cañas Gordas, *Pittier 11061* (CR, US). SAN JOSÉ: C. R. #223 ca. 16–24 km. s. of San Isidro del General, *Almeda 2692* (F, GH, LA, US), *Almeda 2693* (DUKE, LA, MICH, MO, NY, US); 20 km. w. of San Isidro del General, *Davidse & Pohl 1293* (MO, US); Alto La Palmera, Carretera Panamericana, *Jimenez 3741* (CR); vicinity of El General, *Skutch 3964* (A, MO, NY, US); basin of El General, *Skutch 4690* (A, CR, F, MO, NY, US). **Panama.** CHIRIQUÍ: eastern Chiriquí between Hato del Jobo and Cerro Vaca, *Pittier 5414* (US, photo at NY). COCLÉ: vicinity of El Valle along the lower Rio Antón, *Allen 112* (A, MO, NY); El Valle, *Allen 1175* (GH, MO, NY, US); w. slopes of Cerro Pajita in crater of El Valle de Antón ca. 3 mi. n. of El Valle, *Wilbur & Almeda 15607* (DUKE, MICH, MO); Bismark above Penonomé, *Williams 321* (NY, US).

This species exhibits little intraspecific variation in features that tend to be plastic in other taxa. The pendent flowers, straight styles, connivent, linear-subulate anthers, and greatly reduced appendages differ so markedly from other congeners that Kränzlin's initial placement of this entity in *Tibouchina* is understandable. *Centradenia paradoxa* superficially resembles *Tibouchina longifolia* (Vahl) Baillon ex Cogniaux in habit and floral features, but the latter differs consistently in having 5-merous flowers, linear-lanceolate sepals, cochleate seeds, symmetric leaf bases, and adaxial foliar trichomes which are adnate to the epidermis for a portion of their length.

Kränzlin was correct in expressing doubt over the generic assignment of his new species since the specimens known to him lacked mature capsules and seeds. The slender, more or less zigzag stems and caducous nature of the smaller leaf at each node led him erroneously to suggest, however, that this species might be a woody climber with alternate phyllotaxy.

Williams (1963) emphasized the overall similarity of this species to

Centradenia inaequilateralis and suggested that it represented nothing more than a large-leaved variant of the latter, perhaps worthy of infraspecific status. Field studies of these taxa leave no doubt that they should be retained as distinct species. They differ dramatically in several characters, the most notable being foliar size, floral bracts, inflorescences, hypanthia, stamens, and seeds.

The closest relative of *C. paradoxa* appears to be *C. grandifolia* subsp. *grandifolia* with which it shares clavate, echinate seeds and a more or less dichasial inflorescence.

3. *Centradenia floribunda* Planchon, Fl. Serres 5: pl. 453. 1849.

Erect, laxly branched, suffrutescent perennial mostly (12-)20-50 cm., but infrequently as tall as 1.5 m. Cauline internodes terete to subquadrangular, glabrate below but moderately to copiously appressed-pubescent above, the trichomes either smooth or glandular, and prevailingly less than 0.5 mm. long. Principal leaves dimorphic to subequal in each pair, entire, lanceolate, apically acute to attenuate, basally symmetric and attenuate or somewhat oblique, moderately to sparsely appressed-pubescent above with trichomes often restricted to the elevated primary nerves below. Larger leaf at each node 2-10 cm. long and 0.5-3.5 cm. wide, 3-5-plinerved, the three central nerves elevated and conspicuous below, the marginal pair mostly depressed and inconspicuous; petioles 0.8-2.5(-4) cm. long and 1 mm. wide. Smaller leaf at each node usually persistent, 0.5-6 mm. long and 0.5-1.0 mm. wide. Inflorescence terminal, often on lateral shoots, basically paniculate in outline but typically consisting of a cluster of 2-6 elongate racemes diverging from one another \pm basally. Floral bracts thinly membranaceous, reduced in size upward along the raceme, early deciduous, 2-10 mm. long, 0.5-3 mm. wide, linear-lanceolate to obovate, entire, glabrous within and puberulent without, uppermost bracts closely enveloping buds or their pedicels. Pedicels 4-9 mm. long, glandular-puberulent, erect at anthesis but strongly cernuous in fruit. Hypanthia (at anthesis) campanulate, beset with a copious mixture of smooth, appressed, and spreading glandular trichomes. Sepals (on mature hypanthia) erect, broadly deltoid and apically rounded, glabrous within and glandular-puberulent without, 1-2 mm. long and 1.5-2 mm. wide. Petals pale pink to magenta, obovate, entire, sometimes remotely ciliate and shallowly emarginate, 4-11 mm. long and 3.5-9 mm. wide. Stamens strongly dimorphic, alternately dissimilar with prolonged connectives modified ventrally into elaborate upturned appendages, or stamens weakly dimorphic with short connectives and markedly reduced appendages. Pollen 12.5-15 μ m. in diameter. Ovary obovoid, glabrous or sparingly beset with smooth and/or glandular trichomes; the wall elaborated apically into eight compressed, \pm triangular gland-tipped lobes surrounding the stylar base. Style straight or declinate, 4-8 mm. long, stigma punctiform to subcapitate. Hypanthia (at maturity) campanulate to suburceolate, 3-5 mm. long and 2.5-4 mm. wide. Seeds narrowly pyriform to clavate, muriculate to obscurely papillate, mostly 0.5 mm. long.

As presently perceived, *Centradenia floribunda* consists of two allopatric entities herein accorded subspecific recognition. Indistinguishable on vegetative grounds, these taxa are based largely on diagnostic floral characters involving the size, shape, and orientation of anther thecae, connectives, ventral appendages, and style. Williams (1963), on the basis of the limited material then available, indicated that some specimens appeared to be intermediate between the two floral types. My study of this species complex has included all specimens examined by Williams plus collections from additional populations that have accumulated in the interim. Since all specimens are readily assignable to one subspecies or the other, I feel that failure to draw a formal distinction between them would obscure evolutionary tendencies. Unfortunately, this is the only species that has not been studied in the field: the adaptive significance of the geographically correlated floral dimorphism is, therefore, not clear at this time. By extrapolating from what is known about the floral biology of the other species, one may predict that the floral peculiarities are correlated with modally different pollination systems.

3a. *Centradenia floribunda* Planchon subsp. *floribunda*. FIGURE 7.

Centradenia floribunda Planchon, Fl. Serres 5: pl. 453. TYPE: although no type has been either designated or located, I gather from the protologue that this species was described from cultivated material grown from seed that was presumably collected at an unknown locality in Guatemala (lectotype: unnumbered colored plate opposite page 453 of the protologue).

Centradenia floribunda Planchon var. *grandifolia* Cogniaux in Donn. Sm. Bot. Gaz. 20: 286. 1895. TYPE: Guatemala. Amatitlan: Palin, *Donnell Smith* 2645 (holotype: US!; isotypes: F!, GH!, NY!).

Petioles of larger leaf at each node 0.4–1.5(–2.5) cm. long. Petals pale pink, 4–7 mm. long and 3.5–5 mm. wide. Stamens weakly dimorphic to subequal, alternately differing in length, straight or slightly flaring distally and \pm connivent around the style. Larger stamens: filaments 3–4 mm. long; anthers pale yellow, elliptic to elliptic-obovate, 1–1.5 mm. long, 1 mm. wide, thecae smooth and not conspicuously convolute; connective 1 mm. long; appendages yellow, compressed, bilobate or trilobate, upturned or deflexed, 0.5–1.0 mm. long and \pm 0.5 mm. wide. Smaller stamens: filaments 3–3.5 mm. long; anthers pale yellow, ovate to elliptic-ovate, 1–1.5 mm. long, 0.5 mm. wide, thecae smooth, channeled ventrally; connective 0.5 mm. long; appendages yellow, shallowly bilobed, mostly less than 0.5 mm. long. Style straight, 4–6 mm. long, \pm equaling the stamens. Chromosome number: $n = 18$.

Flowering: all year.

DISTRIBUTION. From Volcán Tacaná in eastern Chiapas, Mexico, to the western and central departments of Guatemala, mostly at elevations of 250 to 1800 meters but infrequently as high as 2450 meters. The type collection of *Centradenia floribunda* var. *grandifolia* was reportedly collected at an elevation of 3560 meters. This is questionable and requires

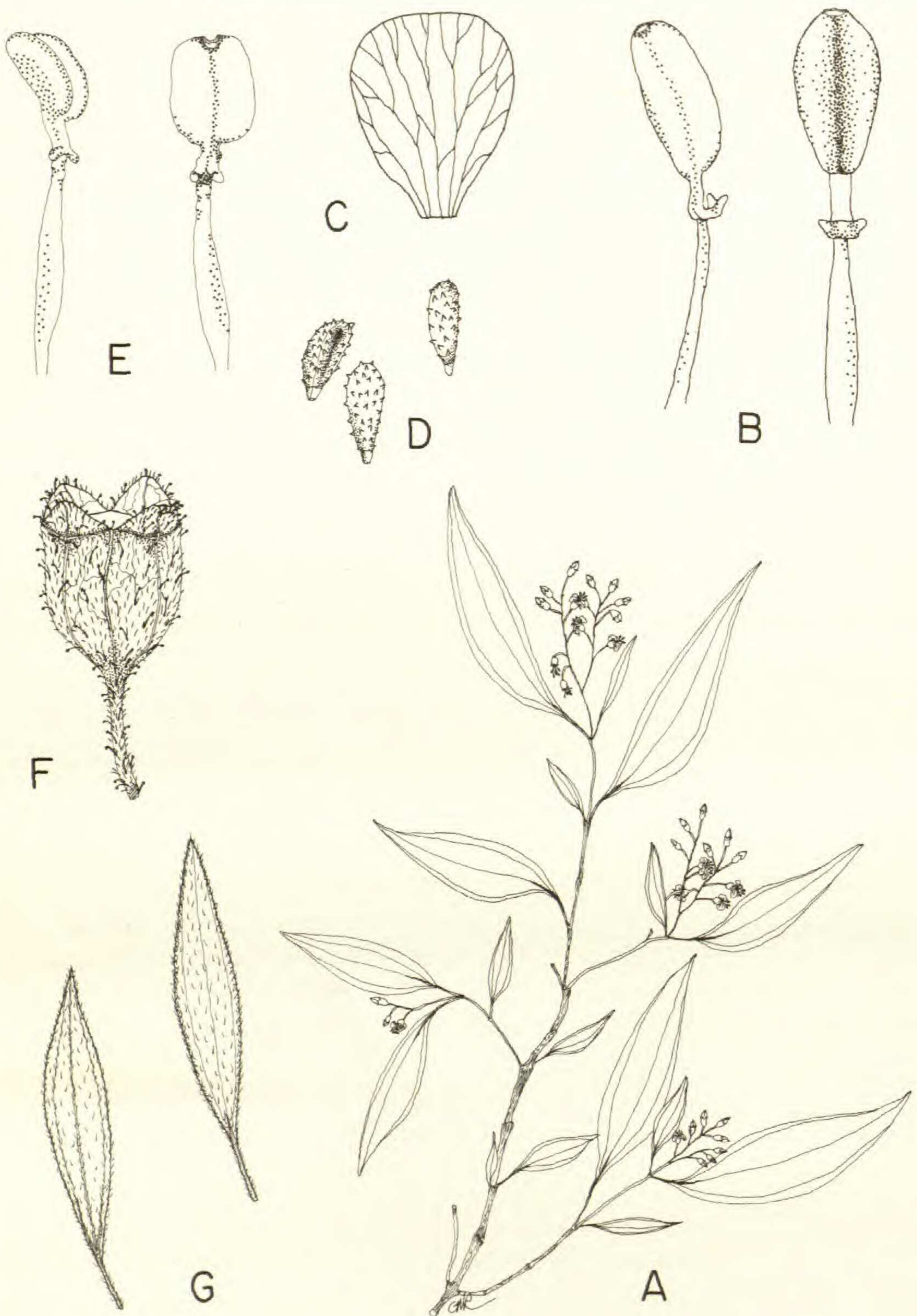


FIGURE 7. *Centradenia floribunda* subsp. *floribunda*. A, habit showing anisophylly, \times ca. $\frac{1}{3}$; B, larger stamens, lateral view (left) and ventral view (right), \times 20; C, petal, \times 4; D, seeds, \times 24; E, smaller stamens, lateral view (left) and ventral view (right), \times 15; F, mature hypanthium, \times 5; G, leaves, abaxial surface (left) and adaxial surface (right). (A-G from *Stone 3092*).

additional collections for confirmation. One other specimen, *Schaffner s.n.* (A) was purportedly collected at Santa Ana in Jalisco, Mexico, a locality unknown for the genus and far removed from the normal range of this species. If the label data on that collection are correct, it would constitute an appreciable westward range extension for *C. floribunda* since it is not known in Mexico from any intervening area west of Volcán Tacaná on the Guatemalan border. Although a few species of flowering plants are known from Jalisco and not otherwise except from Central America or the West Indies (McVaugh, pers. comm.), I am inclined to doubt the authenticity of this record until it is substantiated by recent collections.

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: Volcán Tacaná, *Matuda 2751* (MEXU, MICH, NY). **Guatemala.** CHIMALTENANGO: Concepción, *Johnston 534* (F). CHIQUIMULA: vicinity of Montaña Cebollas, along Rio Lucia Saso ca. 3 mi. se. of Quezaltepeque, *Steyermark 31318* (F). ESCUINTLA: vicinity of Escuintla, *Donnell Smith 2216* (F, GH, MO, NY, US); 1–5 km. e. of CA-9 on road to San Vicente Pacaya, *Harmon 1946* (ENCB, MO); cliffs about Finca Zapote, *Muenschler 12341* (F); along Rio Guacalate, *Standley 58161* (F, NY); between Rio Jute and Rio Pantaleop on road between Escuintla and Santa Lucia, *Standley 63436* (F, NY). GUATEMALA: near finca La Aurora, *Aguilar 222* (F); sand creek ca. 12 mi. ne. of Guatemala City, *Brenckle 47397* (F, NY); banks along Rio Villalobos, *Molina, Burger, & Wallenta 16031* (F, NY, US); arroyo s. of Guatemala on road to Amatitlan, *Standley 62817* (F, MICH, NY). JALAPA: Los Chorros along Rio Pinule ca. 1 mi. w. of San Pedro Pinula, *Steyermark 32936* (F, NY); between Jalapa and La Laguna, *Standley 76899* (F). QUEZALTENANGO: off Hwy. 95 at km. 197, old road to Finca Pirineos, *Stone 3092* (DUKE); lower south-facing slopes of Volcan Santa María between Finca Pirineos and Finca Soledad, *Steyermark 33568* (F); damp thickets near Colomba, *Standley 67983* (F); roadside bank, finca Helvetia, *Skutch 1404* (GH, NY); San Martin, *Shannon 513* (US). QUICHÉ: Cunen, *Heyde & Lux 3332* (MO, US). RETALHULEU: Ajaxa e. of Santa Cruz Mulua, *Standley 88206* (F); along road 5 km. w. of Retalhuleu, *Standley 87353* (F, NY); La Llovizna, *Rojas 232* (MO, US); vicinity of San Felipe, *Maxon & Hay 3535* (NY, US); along Rio Samala, *Donnell Smith 2651* (MO, US). SACATEPEQUEZ: near Las Lajas, *Standley 58143* (F, NY). SANTA ROSA: Teocinte, *Heyde & Lux 4181* (GH, NY, US); Aguacaliente, *Kellerman 7760* (US); vicinity of Chiquimulilla, *Standley 79537* (NY). SUCHITEPEQUEZ: finca El Naranjo, s. slopes of Volcan Santa Clara, 12 km. sw. of Volcan Santa Clara, 12 km. sw. of Lago Atitlan, *Fosberg 27187* (US); near bridge on CA-2 along Rio Mora, *Harmon & Dwyer 3411* (ENCB, MO); vicinity of Mazatenango, *Maxon & Hay 3458* (US); rocky banks at Finca Moca, *Skutch 2065* (F, GH, NY); near Pueblo Nuevo, *Standley 66842* (F); south-facing slopes and barrancas of Volcan Santa Clara, *Steyermark 46790* (F, GH, NY, US).

This subspecies varies markedly in foliar size, number of flowers per inflorescence, and the amount of pubescence on the leaves, cauline internodes, and inflorescences. Large-leafed forms from Amatitlan and Retalhuleu, Guatemala, have been recognized as variety *grandifolia*, but these grade imperceptibly into the typical forms from the same localities and appear to be unworthy of taxonomic status. The distinctive staminal features of this taxon should preclude confusion with all other species. Sterile,

depauperate specimens occasionally approach *C. inaequilateralis* in leaf size and shape, but that species differs in its pronounced anisophylly and size mixture of adaxial foliar trichomes.

3b. *Centradenia floribunda* Planchon subsp. *bernoullii* (Cario ex Cogn.) Almeda, comb. nov. FIGURE 8.

Centradenia bernoullii Cario ex Cogn. DC. Monogr. Phan. 7: 118. 1891. ✓ TYPE: El Salvador, without further locality, *Bernoulli* 2 (holotype: B, destroyed during World War II, photographs: GH!, NY!; syntypes: presumably at GOET, K).

Centradenia floribunda Planchon var. *bernoullii* (Cario ex Cogn.) L. O. Williams, Fieldiana Bot. 29: 552. 1963.

Centradenia perquinensis S. Winkler, Bot. Jahrb. 83: 343. 1965. ✓ TYPE: El Salvador. Morazan: Feuchte Bachschlucht am Zompopero an der Strasse Perquin-Savanetas, *Winkler s.n.* (holotype: herbarium of S. Winkler at TUB; isotypes: F!, ITIC).

Petioles of larger leaf at each node 0.8–2.5(–3.5) cm. long. Petals 7–11 mm. long and 4–9 mm. wide. Stamens strongly dimorphic. Larger stamens: geniculate, filaments declinate, 4.5–6.5 mm. long; anthers deep pink to magenta, linear-oblong, 2.5–3 mm. long, 1 mm. wide, thecae distinctly undulate ventrally; connective 2–3 mm. long; appendages yellow, compressed and ligulate or slightly dilated, linear-oblong to ± obtriangular, apically erose with two terminal, upturned, caudiform processes, 3.5–5 mm. long and 1–1.5 mm. wide. Smaller stamens: ± erect to somewhat incurved, filaments 4–6 mm. long; anthers yellow, linear-oblong, 1.5–2 mm. long, 0.5 mm. wide, thecae undulate; connective 1 mm. long; appendages yellow, ± compressed, narrowly obtriangular and distinctly bifurcate, 1 mm. long. Style declinate, 6.5–8 mm. long, ± opposing the apical pores of the larger stamens.

Flowering: December to January, and perhaps sporadically during other months.

DISTRIBUTION: Sporadic through much of El Salvador, extending north to western and central Honduras, at elevations of 350 to 1800 meters.

REPRESENTATIVE SPECIMENS. El Salvador. AHUACHAPAN: vicinity of Ahuachapan, *Standley* 20282 (NY, US); *Standley & Padilla* 2504 (F); Laguna de las Ninfas near Apaneca, *Winkler s.n.* (F). CUSCATLAN: Cojutepeque, *Shannon* 5035 (F, GH, US). LA LIBERTAD: vicinity of Santa Tecla, *Standley* 23056 (GH, US); s. of Santa Tecla, *Williams & Molina* 15093a (F); moist bank above Colon, *Williams & Molina* 16784 (F). MORAZAN: s. side of Montes de Cacaguatique, *Tucker* 745 (F, MICH, UC, US). SAN SALVADOR: vicinity of San Marcos, *Carlson* 1 (F, GH, NY, UC, US); El Picacho, Volcan San Salvador, *Molina & Montalvo* 21864 (DS, GH, NY). SAN VICENTE: vicinity of San Vicente, *Standley* 21210 (GH, US); *Standley & Padilla* 3402 (F). SONSONATE: vicinity of Izalco, *Pittier* 1945 (US); vicinity of Armenia, *Standley* 23479 (GH, NY, US). HONDURAS. COMAYAGUA: Barranco Trincheras ca. 16 km. from Siguatepeque, *Molina* 7936 (F); Quebrada Montanuelas between Trincheras and Montanuelas, *Molina*

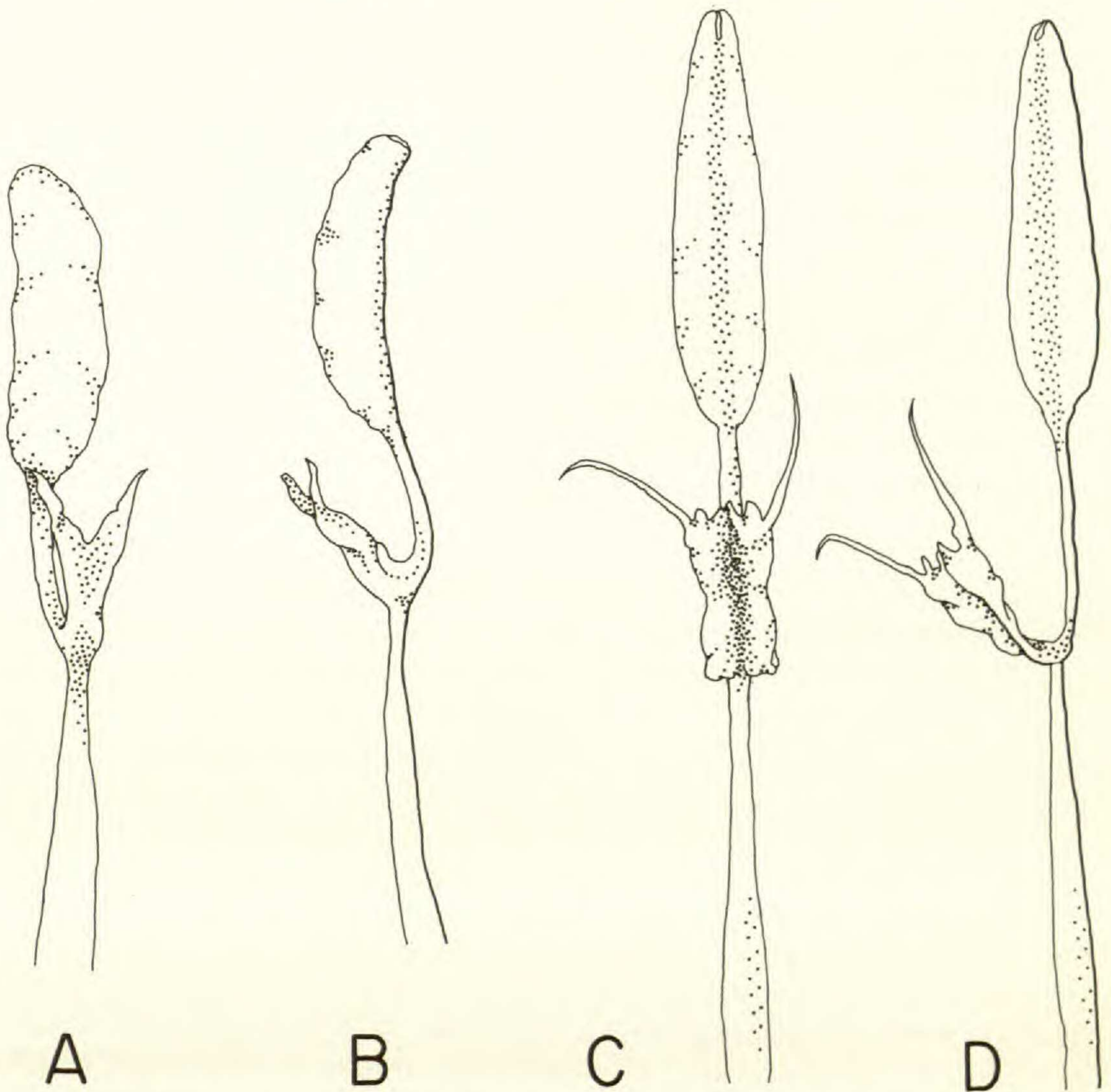


FIGURE 8. *Centradenia floribunda* subsp. *bernoullii*. A & B, smaller stamens, ventral view (left) and lateral view (right), $\times 14$; C & D, larger stamens, ventral view (left) and lateral view (right) showing setose appendage, $\times 14$. (A-D from *Molina & Montalvo 21864*).

10860A (US); La Cocona, 6 km. e. of Siguatepeque, *Molina & Molina 25489* (F, NY); vicinity of Siguatepeque, *Standley 55910* (F, US); 5 km. s. of La Mision, *Williams & Molina 18004* (GH, US); ravine near El Achote above plains of Siguatepeque, *Yuncker et al. 6614* (F, GH, MICH, MO). EL PARAÍSO: Barranco Galeras between Casitas and Cuesta de Galeras, *Molina 8571* (F, US); Quebrada Tapahuasea between Manzaragua and San Lucas, *Molina 18737* (F, NY); Guinope, *Rodriguez 1827* (F). INTIBUCÁ: Cascada de Yamaranguila, *Molina 6344* (F, NY, US); Cordillera Opalaca, between El Pelon and Camaco on road to Gracias, *Molina & Molina 24457* (F); 9 km. e. of La Esperanza along Huise River, *Molina & Molina 25564* (NY). LA PAZ: between Florida and El Cerron ca. 7 km. from Marcala, *Molina 24072* (DS, F); between Sasagua River and Llano de San Antonio, *Molina 24131* (F, NY). MORAZAN: vicinity of Las Mesas, *Swallen 11422* (US); along Quebrada Quemada at km. 21 in vicinity of Cerro de Hule, *Molina 25417* (DUKE, F, MO).

This subspecies is characterized by its linear-oblong anthers, prolonged connectives, and unique staminal appendages. Foliar size appears to be the only character that displays any notable variation. In general, the Honduran populations have narrower linear-lanceolate leaves with symmetric bases that appear very different from the typical element. Although narrow-leaved forms are less frequent in El Salvador, at least one such collection from Morazan formed the basis for Winkler's *Centradenia perquinensis*, a species herein relegated to synonymy.

One unusual collection from the vicinity of Apaneca, El Salvador (*Winkler s.n.*), has narrowly winged, cauline internodes, a rather congested paniculate inflorescence, and large fruiting hypanthia reminiscent of *C. grandifolia*, but the floral and seed characters leave no doubt that it should be assigned to this subspecies.

While there is no strong evidence to suggest which of the subspecies is the most "primitive," I have intuitively favored subspecies *bernoullii* as the most likely candidate. Evolution of the comparatively simple structure and conformation of stamens in subspecies *floribunda* is easily envisaged by a reduction of anthers, connectives, and appendages, coupled with a change in their posture and orientation.

4. *Centradenia grandifolia* (Schlechtd.) Endl. Rep. Bot. Syst. 2: 119. 1843.

Erect, strictly to arcuately branched, suffrutescent perennial, 0.5–1.5 m. tall. Distal cauline internodes semisucculent, strongly quadrangular and conspicuously alate, glabrate to puberulent, the trichomes appressed to spreading, and mostly less than 0.5 mm. long. Plants strongly anisophyllous. Principal leaves thinly membranaceous, entire, basally asymmetric, dark green above and often deeply pigmented below. Large leaf at each node lanceolate to ovate-lanceolate, typically appearing broadly falcate, (2–)5–20(–24) cm. long, 1.5–7 cm. wide, apically acute to acuminate or attenuate, (4–)5–6(–7)-plinerved with a conspicuous network of secondary veinlets, sparsely to copiously pubescent above, but trichomes largely confined to primary and secondary nerves below; petioles 1–13(–22) mm. long, sometimes alate, the wings often extending along the median nerve for $\frac{1}{2}$ – $\frac{2}{3}$ the length of the blade. Smaller leaf at each node commonly deciduous, sessile, narrowly lanceolate to falcate or subulate, 1–12(–25) mm. long and 1–7 mm. wide, glabrous above and puberulent to glabrate below. Inflorescence terminal or axillary, typically a multiflowered (often corymbiform) dichasium 7–18 cm. long, peduncles glabrate or beset with both smooth and glandular trichomes. Floral bracts sessile, deciduous, 2–18(–33) mm. long and 0.5–6 mm. wide, linear-lanceolate to obovate or subulate, enveloping young buds and pedicels, glabrous above, sparsely puberulent below. Pedicels (1–)4–12 mm. long, glabrous or glandular-puberulent. Hypanthia (at anthesis) urceolate to campanulate, glabrous or glandular-puberulent. Sepals (on mature hypanthia) \pm erect, triangular-ovate to truncate or mucronulate, entire to remotely crenulate, ciliate,

1–3 mm. long. Petals pink or white, obovate, entire to obscurely erose or crenulate, often fringed with glandular trichomes, 5–11 mm. long, 4–8 mm. wide. Stamens dimorphic. Larger stamens: geniculate; filaments 4.5–7 mm. long, anthers pink to magenta, linear-oblong to subulate, 4–5.5 mm. long and 1 mm. wide, thecae undulate; connective 2–5.5 mm. long; appendages yellow, \pm horizontal, clavate, dilated and bluntly bifurcate distally, 1.5–3 mm. long. Smaller stamens: erect; filaments 4–6 mm. long; anthers and appendages yellow, 2–4.5 mm. and 0.5–1 mm. long, respectively, otherwise similar to larger anthers. Ovary ovoid to obovoid, puberulent, the wall elaborated apically into four scalelike outgrowths surrounding stylar base. Style 7–12.5 mm. long, declinate, and opposing the geniculate staminal whorl. Hypanthia (at maturity) 4–8 mm. long and 4–8 mm. wide. Seeds 0.5–1 mm. long, clavate to dolabriform, echinate, muricate, or with low, domelike processes.

The extensive morphological variability exhibited by *C. grandifolia* is comparable to that of *C. inaequilateralis*; unlike that species, it falls into two discontinuous, geographically definable patterns, thus justifying subspecific status. Basic differences between the two subspecies reside in hypanthial and sepal shape, the surface pattern and shape of seeds, and perhaps less significantly in petal color.

4a. *Centradenia grandifolia* (Schlecht.) Endl. subsp. *grandifolia*.
FIGURE 9 A–E, G–I.

Rhexia grandifolia Schlecht. Linnaea 13: 429. 1839. ✓ TYPE: Mexico. Veracruz: Cuesta Grande de Chiconquiaco, *Schiede s.n.* (holotype: presumably at B and destroyed during World War II; isotype: NY!).

Centradenia salicifolia T. S. Brandege, Univ. Calif. Publ. Bot. 4: 379. 1913. ✓ TYPE: Mexico. Veracruz: Sierra Madre between Misantla and Naolinco, *Purpus 6103* (holotype: UC!; isotypes: F!, GH!, MO!, NY!, US!).

Centradenia chiapensis T. S. Brandege, Univ. Calif. Publ. Bot. 6: 501. 1919. ✓ TYPE: Mexico. Chiapas: Cerro del Boqueron, *Purpus 6978* (holotype: UC!).

Mature hypanthia urceolate, broadest at the middle, 4–8 mm. long, glabrous or glandular-puberulent, accrescent and bladderly, loosely enveloping the ovoid ovary. Sepals triangular-ovate, apically rounded, (1–)2–3 mm. long. Petals pink. Pollen 16.2–17.5 μ m. in diameter. Seeds clavate, echinate, the setose projections often appearing glandular. Chromosome number: $n = 18$.

Flowering: all year.

DISTRIBUTION: Hidalgo, Puebla, Veracruz, and Chiapas in southeastern Mexico, to San Marcos, Suchitepequez and Quezaltenango in western Guatemala, with southern disjunct populations in the provinces of Alajuela, Cartago, and San José, Costa Rica, at elevations of 1300 to 2500 meters. Molina (1975) includes this taxon in his enumeration of Honduran plants, but the collection upon which his record was presumably based (*Molina 18738*) matches typical *C. floribunda* subsp. *bernoullii* in all details. To date, I have seen no authentic material of *C. grandifolia* from Honduras.

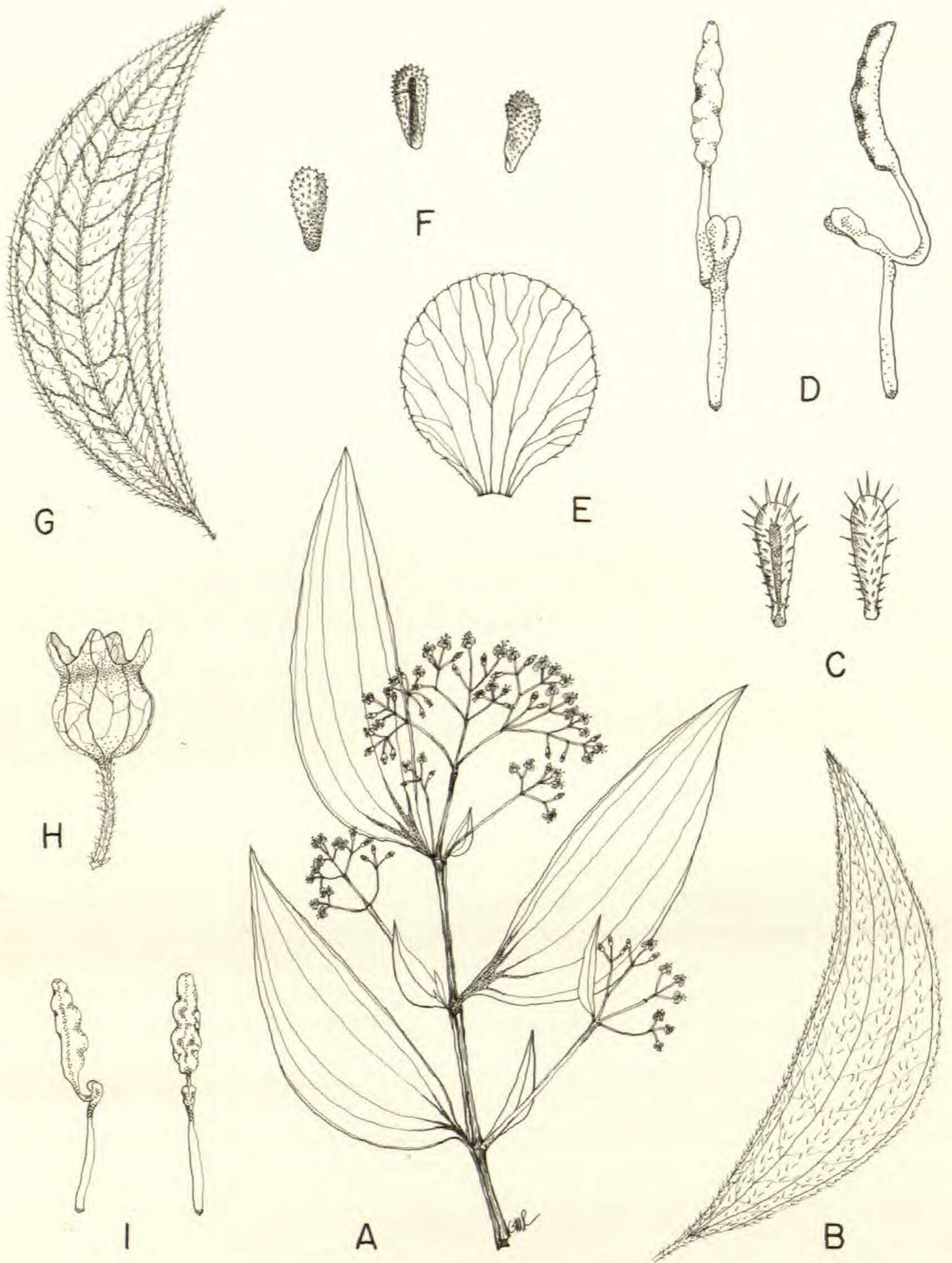


FIGURE 9. A-E, G-I, *Centradenia grandifolia* subsp. *grandifolia*. A. habit, showing quadrangular stem and dichasial inflorescence, \times ca. $\frac{1}{3}$; B, leaf, showing adaxial surface, \times $\frac{1}{2}$; C, seeds, ventral view showing raphe (left) and dorsal view (right), \times 15; D, larger stamens, showing prolonged connective and bilobed appendage, ventral view (left) and lateral view (right), \times 4; E, petal, \times 3. F, *Centradenia grandifolia* subsp. *brevisepala*, seeds, \times 11. Subsp. *grandifolia*, G, leaf, showing abaxial surface, \times $\frac{1}{2}$; H, hypanthium, \times 2; I, smaller stamens, lateral view (left) and ventral view (right), \times 4. (A-E, G-I from *Almeda & Flowers* 2080; F, from *Donnell Smith* 1540).

REPRESENTATIVE SPECIMENS. **Costa Rica.** ALAJUELA: Tapesco de Zarcero on road to Quesada, *Smith 251* (US); Zapote de San Carlos, *Smith PC315* (F); vicinity of Naranjo, *Stork 1843* (F, MICH). CARTAGO: ca. 20 km. se. of Cartago, *Godfrey 66136* (FSU); km. 49 on Panamanian Hwy. s. of Tejar, *Lent 262* (F, NY); ca. 6 km. n. of El Empalme towards Cartago, *Wilbur, Almeda, & Luteyn 16190* (CAS, DUKE, F, LL, MICH, MO, US). SAN JOSÉ: ca. 27 km. sse. of Cartago and 51 km. nnw. of Villa Mills, *Almeda 2677* (F, LA, MO, UC, US); ca. 9 km. beyond San Isidro del General, *Almeda & Flowers 2080* (CR, DUKE, F, MICH, MO, UC); 25 km. n. of San Isidro del General, *Burger & Leisner 7051* (CR, NY); 14 km. s. of División, *Davidse & Pohl 1404* (CR, MO, US); vicinity of El General, *Skutch 4205* (A, MO, NY, US); vicinity of Santa María de Dota, *Standley & Valerio 44093* (F, US); 16 mi. n. of San Isidro, *Wilbur & Luteyn 19005* (DUKE, LA). **Guatemala.** QUEZALTENANGO: slopes of Volcan Zuñil above Agual Amargas, *Standley 65325* (F, GH, NY); Cumbre de Tuilacan, sw. of San Martín Chile Verde, *Standley 67764* (F); region of Boxantin, se. of San Martín Chile Verde, *Standley 83759* (NY); along Rio Samala, near Santa María de Jesus, *Standley 84577* (F); above Mujulia, between San Martín Chile Verde and Colomba, *Standley 85451* (F); along Rio Samala, between Santa María de Jesus and Calahuache, *Steyermark 33877* (F, NY). SAN MARCOS: 9.6 mi. w. of San Pedro Sac towards San Rafael Pie de la Cuesta, *Luteyn & Almeda 3474* (DUKE, F); slopes along Rio Vega on ne. portion of Volcán Tacaná near San Rafael, *Steyermark 36343* (F, NY); nw. slopes of Volcán Tajumulco, 6 mi. sw. of Tajumulco, *Steyermark 36644* (F); 5 mi. e. of San Rafael en route to San Marcos, *Whiffin & Rodriguez 430* (TEX). SUCHITEPEQUEZ: sw. slopes of Volcan Zuñil between finca Montecristo and finca Asturias, *Steyermark 35312* (F, NY). **Mexico.** CHIAPAS: Union Juarez, Volcán Tacaná, *Matuda 3001* (F, GH, MEXU, MICH, MO); Tapalapa, Blanca Rosa, *Miranda 6559* (MEXU); Cerro del Boquerón, *Purpus 7059* (GH, NY, UC). HIDALGO: 2 km. s. of Tlanchinol, *Rzedowski & Madrigal 29453* (ENCB). PUEBLA: near summit of El Cerro de Cuhuatepetl ca. 15–16 km. sw. of Campo Experimental de Hule, *Santos 3665* (MICH, US); falls of Necaxa, district of Huauchinango, *Roby s.n.* (US). VERACRUZ: above Canada del Huerfano, *Gómez-Pompa 1822* (MEXU); Cerro Punta Coscomat, *Matuda 1506* (MEXU, MICH); Santa Rita, Sierra de Chiconquiaco, *Nevling & Gómez-Pompa 19* (GH, MEXU); 5 km. s. of Coscomatepec, *Rzedowski 19075* (ENCB, MICH, US); El Haya, municipio de Yecuatla, *Ventura 3286* (ENCB); municipio de Naolinco, *Ventura 10400* (ENCB).

This well-marked subspecies is readily distinguished by its strongly quadrangular to alate stems, dimorphic androecium, urceolate hypanthia, and echinate seeds. The disjunct population structure of this taxon has undoubtedly promoted some inter-population differentiation. Many of the Costa Rican populations have larger leaves (16–23 × 5–7 cm.), glabrous hypanthia, and denser pubescence on the inflorescence and upper foliar surfaces, but these variations are also displayed by a collection (*Rzedowski & Madrigal 29453*) from the northernmost locality for the species in Hidalgo, Mexico.

Specimens from Chiapas and Veracruz, to which Brandege assigned specific epithets, undoubtedly belong here but differ from typical plants in their narrower, glabrate leaves and few-flowered inflorescences with shorter internodes.

The most distinctive variant from Puebla, Mexico (*Santos 3665*) has subquadrangular cauline internodes, reportedly white petals, basally cuneate, glabrous leaves, and broadly campanulate hypanthia crowned by rounded, deltoid sepals. I have tentatively assigned this collection to the typical subspecies. Additional material with mature capsules and seeds, however, may necessitate a reappraisal of its taxonomic status. Although variants of this subspecies often differ strikingly in appearance, it seems evident from the constancy of such unifying characters as the flowers, hypanthia, and seeds that we are dealing with many localized expressions of a polymorphic taxon.

4b. *Centradenia grandifolia* (Schlecht.) Endl. subsp. *brevisepala*
(Gleason) Almeda, comb. nov. FIGURE 9F.

Centradenia grandifolia var. *brevisepala* Gleason, *Phytologia* 1: 340. 1939.
✓TYPE: Guatemala. Alta Verapaz: along trail to Rubel Cruz cave, 3–4 km. w. of Finca Pansamala, *Stuart 15* (holotype: MICH!).

Mature hypanthia campanulate, broadest distally at the torus, 6–7 mm. long, glabrous, not at all accrescent or bladderly, but closely enveloping the obovoid ovary. Sepals depressed-ovate, apically truncate to mucronulate, 1–2 mm. long. Petals white. Pollen 12.5–13.7 μm . in diameter. Seeds \pm dolabriform, muricate or with low, dome-shaped processes.

Flowering: December to April.

DISTRIBUTION. Known only from a few scattered localities in Alta Verapaz, Guatemala. Reportedly collected at an elevation of 3800 feet.

REPRESENTATIVE SPECIMENS. Guatemala. ALTA VERAPAZ: Pansamala, *Donnell Smith 1540* (US); trail to Senahú, *Goll 168* (US); vicinity of Pansamala, *von Tuerckheim 883* (US); finca Trece Aguas, *Wilson 184* (F).

This rarely collected, presumably localized subspecies is known from only five collections, the most recent gathered in 1939. During a recent visit to the type locality and surrounding areas, I was unable to locate any populations of this taxon. It would be premature, however, to suggest that it is rare or on the verge of extinction, for many areas of Alta Verapaz await thorough botanical exploration.

A case could be made for recognizing this taxon at the specific level. Unlike Williams (1963), I have chosen not to adopt this course of action for I feel that it would misrepresent our current knowledge of this entity and obscure its overriding floral and vegetative similarities to the typical subspecies.

UNCERTAIN SPECIES

Centradenia ovata Kl. in Otto & Dietr. *Allg. Gartenz.* 19: 354. 1851. TYPE: Central America, without further locality, *Warszewicz s.n.* (holotype: presumably at B and destroyed).

The generalized original description coupled with the lack of authentic material prohibit unequivocal disposition of this epithet. In the treatment of *Centradenia* by Klotzsch, *C. ovata* was the only constituent of a presumed section (*Homalophyllum*) characterized by subequal, persistent, basally more or less symmetric leaves. This, together with the protologue description of the inflorescence as “. . . cymis terminalibus trichotomis . . . ,” suggests that this species may be synonymous with *C. floribunda*. Unfortunately, the imprecise collection locality and the absence of a description of the stamens preclude assignment of *C. ovata* to either of the two subspecies of *C. floribunda* recognized in this treatment.

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